PERSPECTIVES IN ETHOLOGY

Volume 13

Evolution, Culture, and Behavior

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PERSPECTIVES IN ETHOLOGY

Volume 13

Evolution, Culture, and Behavior

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Springer Science+Business Media, LLC

The Library of Congress has cataloged this title as follows:

Perspectives in ethology.–Vol. 1—New York: Plenum Press, 1973–
v.: ill.; 24 cm.

Irregular.

Includes bibliographies and indexes.
Editors: v. 1– P.P.G. Bateson and P.H. Klopfer
ISSN 0738-4394 = Perspectives in ethology.

1. Animal behavior—Collected works. I. Bateson, P.P.G. (Paul Patrick Gordon, 1938– II. Klopfer, Peter H. [DNLM: W1 PE871AN]

QL750.P47 591.5'.1—dc19 86-649219

AACR 2 MARC-S

Library of Congress [8610]

ISBN 978-1-4613-5447-5 ISBN 978-1-4615-1221-9 (eBook)
DOI 10.1007/978-1-4615-1221-9

©2000 Springer Science+Business Media New York
Softcover reprint of the hardcover 1st edition 2000
Originally published by Kluwer Academic / Plenum Publishers

http://www.wkap.nl/

10 9 8 7 6 5 4 3 2 1

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PREFACE

The relations between behavior, evolution, and culture have been a subject of vigorous debate since the publication of Darwin's *The Descent of Man* (1871). The latest volume of *Perspectives in Ethology* brings anthropologists, ethologists, psychologists, and evolutionary theorists together to reexamine this important relation. With two exceptions (the essays by Brown and Eldredge), all of the present essays were originally presented at the Fifth Biannual Symposium on the Science of Behavior held in Guadalajara, Mexico, in February 1998.

The volume opens with the problem of the origins of culture, tackled from two different viewpoints by Richerson and Boyd, and Lancaster, Kaplan, Hill, and Hurtado, respectively. Richerson and Boyd analyze the possible relations between climatic change in the Pleistocene and the evolution of social learning, evaluating the boundary conditions under which social learning could increase fitness and contribute to culture. Lancaster, Kaplan, Hill, and Hurtado examine how a shift in the diet of the genus *Homo* toward difficult-to-acquire food could have determined (or coevolved with) unique features of the human life cycle. These two essays illustrate how techniques that range from computer modeling to comparative behavioral analysis, and that make use of a wide range of data, can be used for drawing inferences about past selection pressures.

As culture evolves, it must somehow find its place within (and also affect) a complex hierarchy of behavioral and biological factors. The three essays by Ghiselin; Odling-Smee, Laland, and Feldman; and Eldredge accordingly center on these hierarchies and how they should be conceptualized. Ghiselin draws on his individuality thesis to explore analogies and disanalogies between species, language, and culture. Odling-Smee, Laland, and Feldman show how the inclusion of cultural factors in a hierarchy of

determinants of evolution significantly enriches current evolutionary theory. Eldredge explores in detail possible parallels between biological evolution and the evolution of cultural artifacts, stressing common patterns of stability and change as well as the relevance of interaction among economic and informational hierarchies.

As these essays make clear, behavior plays a crucial role in the hierarchy of factors that contribute to biological and cultural evolution. How individual behavior should be analyzed, however, has been, for better or worse, the traditional province of psychology. The next three contributions explore alternative proposals for describing or explaining behavior. The essay by Tonneau and Sokolowski provides some warning, with a criticism of the metaphorical notion of selection applied to behavior. Baum presents a strictly behavioral analysis of cultural units and cultural transmission; his discussion of self-control and its relation to culture should prove provocative to the reader. Thompson and Derr assault the barrier between biological and cultural phenomena often raised by philosophers of mind. They argue that intentionality, far from being a unique property of human linguistic behavior, is a universal property of biological regulatory systems.

The interaction of human behavior with environmental and cultural factors has generated some particularly complex results. The last essays of this volume, by Brown and Hinde, address two of these phenomena. Drawing on a rich variety of data, Brown argues that a proper account of the evolution of music will necessarily appeal to group selection. We think that his essay will prove particularly provocative; in making the claim that group selection is an important contributor to human music making, he is going against the received wisdom of both evolutionary psychology and biomusicology. Finally, Hinde discusses how religion can arise from interactions among basic human propensities, which stresses once again the need for an adequate analysis of behavioral units in any theory relating evolution and culture.

The present volume is perhaps best characterized by its interdisciplinary nature and reliance on an eclectic range of approaches. One theme which naturally emerged from the collected essays, however, is that of causation versus analogy. Phenomena defined at multiple levels can in principle be studied in two different ways, "vertical" and "horizontal." The "vertical" strategy tries to directly specify causal relations holding among levels, whereas the "horizontal" approach looks for parallels among levels, in the hope of isolating shared causal properties. Odling-Smee, Laland, and Feldman's essay most directly stands for the vertical strategy, while Tonneau and Sokolowski explicitly warn against the perils of a loose selectionist analogy among levels. The essays that probe other parallels between evolution and culture appropriately call attention to the general limits of analogy (Ghiselin) or carefully note in which respects the proposed analogy

is expected to break down (Eldredge). The other themes of economics, optimization, and stability (Depew & Weber, 1997), when not explicitly mentioned, lurk in the background of any treatment of culture and behavior in relation to natural selection.

Ever since its inception by Patrick Bateson and Peter Klopfer in 1973, the series *Perspectives in Ethology* has been dedicated to encouraging fresh perspectives and ideas. Accordingly, the editors' role has not been to censor or direct authors, but to encourage them to make the strongest and clearest expositions of their views. The informal contract between the editors and the authors is that editors may offer any suggestion that they like, and authors may reject or accept any suggestion the editors make. Some authors thus chose to work closely with the editors, whereas others developed their essays much more independently.

Aside from the authors themselves, we would like to thank two participants at the Guadalajara symposium, Gary Greenberg and Slobodan Petrovich, who did not contribute papers to this volume but whose presence enriched the conference. We also are indebted to our Editorial Assistant, Joyce Lee, and to our Editor at Kluwer Academic/Plenum Publishers, Michael Hennelly, for their unflagging assistance and patience. The symposium that served as the initial basis for this volume could not have seen the light of day without the support of the University of Guadalajara and Emilio Ribes's unmatched determination to nurture the science of behavior. Finally, the help of the Secretaría de Educación Pública de México, which generously funded the publication of this book, is gratefully acknowledged.

By the time this volume reaches its readers, planning will be well under way for the conference that will serve as the basis for the next volume of *Perspectives in Ethology*. Because no other dispute among ethologists has so confused and disordered our field, this volume—the last under the present series editor—will be dedicated to the group selection controversy. Readers interested in participating in this project should contact Nicholas Thompson at nthompson@clarku.edu.

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Chapter 1

BUILT FOR SPEED: PLEISTOCENE CLIMATE VARIATION AND THE ORIGIN OF HUMAN CULTURE

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1. INTRODUCTION

The evolution of humans is a major event in the Earth's biotic history. Never before has a single species of organism so dominated the planet. Hunting and gathering people penetrated to nearly every habitable scrap of the Earth's surface by the end of the Pleistocene. Beginning about 10,000 years ago, food plant production, and its evolutionary sequelae, have made us a geochemical and geophysical force to be reckoned with. Most accounts of human origins take this ecological dominance as a sign of a qualitatively new and superior form of adaptation and ask, what evolutionary breakthrough led to the unique human adaptive complex—tool making, language, complex social organization, and other aspects of culture.

More recently, behavioral ecologists (Smith & Winterhalder, 1992) have taken a different view of human evolution. They argue that humans

Perspectives in Ethology, Volume 13: Evolution, Culture, and Behavior
edited by Tonneau and Thompson, Kluwer Academic/Plenum Publishers, New York, 2000

are just, as Foley (1987) put it, "another unique species." According to the theory of evolution by natural selection, change results from adaptation to local environments. Scholars in this tradition are suspicious of granting human culture and its products special status. Rather than being a history of a breakthrough to a new adaptive plane, human evolution is more likely a history of adaptation to local environments that happens to have resulted in our current ecological dominance by accident.

Evolutionary psychology is an active research program. Several of the practitioners of this research program believe that much human behavioral variation is the evoked product of innate structure in the mind and minimize the role of cultural transmission (Thornhill, Tooby, & Cosmides, 1997; Pinker, 1997; in contrast see Nisbett & Cohen, 1996). They argue that we should be able to infer the cognitive adaptations that characterize human minds from the challenges of living as a hunter-gatherer in the Pleistocene. On this view, cognitive adaptation to the Pleistocene should take the form of many innate modular algorithms, each designed to solve a particular adaptive problem posed by occupying such a niche. Much variation in human behavior, on this view, results from the same innate modules expressed in different environments. In other words a substantial fraction of human behavior across space and time results from the contingent decisions made in the different environments.

Most social scientists imagine a much larger role for transmitted culture in explaining human behavioral diversity. According to this view, what most distinguishes human cognition from that of most other animals is our capacity to transmit large amounts of information culturally, by teaching and imitation. Sophisticated innate cognitive structures are certainly necessary make such transmission possible and to guide it in adaptive directions. However, these innate structures have the effect of setting up a rather general-purpose adaptive system, which enables human populations, using a stunning diversity of culturally transmitted technologies and social institutions, to live practically anywhere on earth. Is there anything about Pleistocene environments that would have favored the evolution of such an extra-genetic, general-purpose adaptive system?

The deterioration of the Earth's climate during the Pleistocene ice age is a major event in the history of the planet's physical environment. Over the last 6 million years, the climate has gotten colder, drier, and more variable. Geology records several other glacial episodes, but the most recent prior one ended 250 million years ago, well before the age of the dinosaurs (Lamb, 1977: 296). Theoretical models of cultural evolution suggest that social learning enhances ability to respond to temporal and spatial variations in the environment. Cultural evolution allows speedy tracking of a rapidly fluctuating environment because it supplements natural selection with learning and other psychological forces. The main hypothesis in this

paper is that social learning is a specific adaptation to Pleistocene climate deterioration. Many animal lineages seem to have taken advantage of the potential of simple forms of social learning. In many respects, human culture is nothing more than a straightforward adaptation to climatic deterioration. However, humans do differ from proto-cultural animals in having the ability to evolve complex, multi-part cultural traditions that must evolve cumulatively, normally over many generations. Technology and social organization furnish many examples of complex traditions that evolve by descent with modification like complex organic adaptations (albeit at a faster rate), whereas other animals have little or no ability to acquire complex traditions. Many aspects of human cognition probably evolved in parallel with the other recently encephalized mammalian lineages, but a complete explanation must deal with our unique dependence on complex traditions.

If the hypothesis here is correct, the central issues of human evolution are how the capacity for complex culture arose from simpler precursors and why our species is unique in possessing what appears to be a rather generally successful adaptation. The correlation between the deteriorating environment of the last few million years and brain size enlargement in mammals generally is strong. This pattern supports the theoretical argument that speed of evolution is the central adaptive advantage of social learning. However, it makes the central puzzle of humans more pointed. If many mammals possess the basic proto-cultural preadaptation for complex culture, why has only our species gone on to acquire the capacity for complex culture? Theoretical models suggest some reasons why the evolution of complex culture may be inhibited until some key preadaptation—more likely a succession of preadaptations—in addition to proto-culture occurs, finally resulting in the breakthrough to culture on the human scale of sophistication.

Reconstructing the evolution of any given lineage involves taking account of poorly understood historical contingencies, requiring some speculative leaps to produce an account of what happened. Nevertheless, explanations of particular historical trajectories are not inherently unscientific (Hull, 1992; Boyd & Richerson, 1992). Every speculation is a hypothesis to be tested, and, indeed, clever investigators often find a way to do so. Sparse data and the inherent unpredictability of evolutionary phenomena do limit, perhaps sharply limit, the detail to which reconstruction can aspire. However, we can reasonably hope to understand the general processes that shaped our evolution in the face of these limitations. One test that any acceptable theory of human evolution must pass is a fit to the large-scale patterns of the paleontological and paleoenvironmental records. This chapter uses such data to test predictions stemming from the general evolutionary properties of systems of social learning and human culture.

2. CULTURE AS AN ADAPTATION TO VARIABLE ENVIRONMENTS

2.1. Social Learning: A Response to Variability Selection

Potts (1996: 231–238) has argued that the fluctuating climates of the Plio-Pleistocene have imposed a regime of what he calls "variability selection" on the Earth's biota. When environments vary, Potts argues, "genetic variations favor open programs of behavior that vary and extend the adaptive possibilities of the individual. These are conserved in the gene pool over time because of the inconsistency in the short-term effects of natural selection. Organisms eventually build up an inheritance system that enables them to buffer larger and larger disturbances in the factors governing survival and successful reproduction" (Potts, 1996: 237; see also Davies et al., 1992). This interesting supposition provides no detail about mechanism. Social learning is a mechanism for adapting to variable environments that may increase dramatically under variability selection. Odling-Smee (this volume) traces out in some detail how the genetic and social transmission might coevolve under an extended regime of variability selection.

Testing this idea is a formidable challenge. Certainly not every lineage on the earth responded to the onset of glacial fluctuations by evolving social learning. Further, humans are the only species to respond to the ice age by evolving the very complex forms of social learning usually given the term "culture." The unique importance of culture in humans is an embarrassment the hypothesis. How can an environmental event that affected the entire earth account for the evolution of one species' peculiar adaptation? The skeptic might ask, if social learning is an adaptation to the Pleistocene, why aren't many species capable of human-like feats of social learning? Is there any evidence that social learning has anything to do with climatic deterioration? How does social learning fit into a pattern of responses to variability selection if indeed this concept is useful?

The hypothesis that climatic variability drove the evolution of human culture derives from the study of theoretical models of the processes of cultural evolution. These models are meant to mimic several aspects of culture. They ask, under what environmental circumstances is a capacity for social learning an adaptive advantage? Like any other adaptation, social learning has costs and benefits, and selection will tend to reach a reliance on social learning that optimizes fitness. What is the basic shape of the adaptive tradeoffs for such systems? A common theme in the results of many models is that social learning is an effective adaptation to spatially and temporally variable environments (Boyd & Richerson, 1985). The models suggest that social learning should commonly arise as an adaptation to variable

environments whenever there is an opportunity to learn from more experienced conspecifics.

Most of these models are so basic that they apply equally to simple systems of animal social learning based on stimulus or local enhancement (Galef, 1988) and to the sophisticated systems of imitation used by humans, and perhaps a few other animals, to create complex cultural traditions. Hence most of what follows uses terms like "social learning" and "culture" as if they were synonyms. The difference is important, however. Human culture based upon rather free imitation supports massive amounts of social learning. Although simple social learning seems to be very common, complex culture based on imitation is much rarer (Moore, 1996). Some of the models suggest why the evolution of complex culture may present a special problem. The issue of complex traditions is discussed explicitly at the end of the chapter.

2.2. Simple Models of Social Learning

One of the most important general features of systems of social learning is that they are systems for the inheritance of acquired variation. What individuals learn for themselves others can acquire by social learning. Our (Boyd & Richerson, 1985) models of this process set up the basic adaptive calculus for a system of inheritance of acquired variation. To learn for itself, an animal will have to expend time and energy in learning, incur some risks in trials that may be associated with large errors, and support the neurological machinery necessary to learn. Social learning can economize on the trial and error part of learning; if offspring learn from parents or other conspecifics, they can avoid repeating their mistakes. With social learning, it may also possible to economize on neurological machinery. Individual learning does not need to be as powerful if most individuals can rely upon social learning most of the time, turning to individual learning only if something indicates that a behavior copied from an experienced conspecific is seriously awry. Or, an animal can use the same neurological machinery to maintain more behaviors to a higher standard of adaptation. Natural selection ought to "tune" capacities for individual and social learning to maximize fitness in the face of their costs and benefits. There is also the alternative of transmitting innate patterns of behavior and foregoing phenotypic flexibility to a greater or lesser degree.

Because a mechanism of phenotypic flexibility, learning, is coupled to a scheme for acquiring the results of such learning by others, a socially transmitted behavior evolves in response to the Lamarckian pressure of learning as well as the pressure of natural selection (on the socially transmitted variation). We label the Lamarckian effect "guided variation"

because it acts as an adaptively non-random form of mutation. Guided variation, using innate decision rules, causes a population's behavior to track environmental change in time or space more accurately than can genes that only respond to selection. In the human case, cultural rules, or mixed innate and socially acquired judgments, may act to guide variation for other behaviors. Thus, natural selection on genes can favor the evolution of a social learning system in appropriately variable environments.

The rest of this section describes two of the models we have used to more rigorously test the logic of these intuitive claims. Readers who already find the intuition compelling and the description of models tedious may wish to skip the rest of this section. Be warned, however, that theorists have already uncovered a number of subtle dynamic problems in systems of social learning (e.g. Rogers, 1989; Boyd & Richerson, 1996). As in evolutionary biology, the intricacies of cultural evolution and gene-culture coevolution frequently defy intuition and verbal reasoning, motivating the use of formal mathematical models.

To test the logic of the claim that systems of social learning are adaptive in variable environments, we constructed very basic models of the individual/social learning process along the following lines: Suppose that the individual learning process is the primitive state. Virtually all animals show at least rudimentary abilities to learn. When animals like birds and mammals come to have extended maternal care, they have the opportunity to learn socially. The models assume that individuals have two sources of information, their own experience and the vicarious experience of individuals with whom they are in social contact. Using two different kinds of models, one based on quantitative characters (Boyd & Richerson, 1985: Ch. 4), and another based on discrete characters (Boyd & Richerson, 1989), we investigated how selection might optimize the relative dependence on the two sources of information.

According to the *discrete character model*, organisms live in one of two environments (e.g., wet or dry) and can express one of two behaviors (e.g. forage collectively or solitarily). There is a fitness benefit for behaving correctly (forage collectively if environment dry, forage alone if wet). Individuals collect some more or less error-prone information about the state of the environment by individual learning. They can also opt to imitate another individual. The degree of dependence on social versus individual learning is controlled by a confidence-interval-like learning threshold, d, to be set by selection at an optimal point (Figure 1). While growing up, individuals gain some idea of the state of the environment. Because of the noisiness of the environment and the inevitable limitations of individuals' observational capabilities, their conclusions as to whether the environment is in the wet or dry state will not necessarily be correct. Even if the

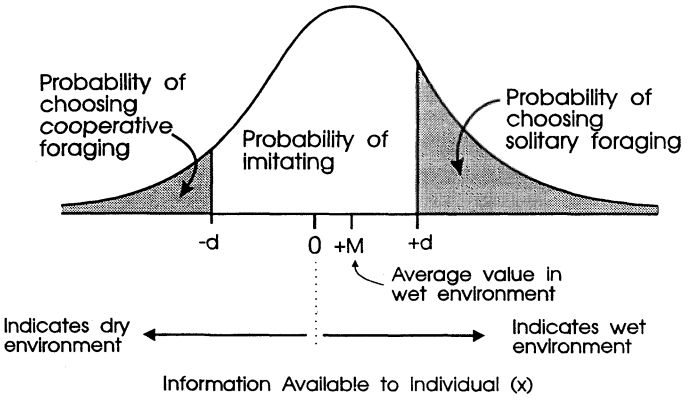

Figure 1. The effect of the learning threshold (d) on the probability of acquiring the best behavior by individual learning or tradition. The curve shows the probability of obtaining a given estimate, x, of the average difference in yield between two environments from a small sample of years of experience of a young forager, assuming that the environment really is in a certain state, wet in this case. The task of the young forager is to decide what to do. If experience seems to show that the environment is indeed rather wet ($x > d$) the forager opts to forage alone. If experience seems to indicate that the environment is dry ($x < -d$), our forager, incorrectly in this case, opts to forage cooperatively. If experience is ambiguous ($-d < x < d$), the young forager follows tradition (adopts parent's behavior). The width of the curve is a measure of the quality of information available from individual learning. In the curve illustrated, individual learning is fairly error prone, and selection is likely to favor setting wide values of d so as to avoid the chance of making an error based on noisy personal experience. However, if the environment is changing rapidly enough, it may be better for young foragers to depend on their own experience in spite of the risks because the risk that their parents are out of touch is also great (from Boyd & Richerson, 1989). First published in Lectures on Mathematics in the Life Science, published by the American Mathematical Society.

environment is dry on average, some individuals will experience an unusual run of rainy years. These individuals are vulnerable to mistakenly deciding that the state of the environment is wet when it is really dry. The confidence parameter d tells us how heavily individuals weigh their noisy samples. If d is large, individuals look for quite definitive evidence that the environment really is in the wet or dry state, say entirely quite wet or quite dry during their formative years. If they do not see such evidence, and most will not if the evidence available to individuals comes from an environment with noisy variation, they imitate an experienced individual of the parental generation, such as their mother. If d is small, information from personal experience is virtually always deemed definitive, and learners depend almost entirely on their personal experience.

The potential advantage of social learning stems from the population level properties of the learning system. In a spatially or temporally varying world, some mixture learning and social learning is generally advantageous. In a noisy world, an evolving population is tending to integrate the experiences of many individuals. One can be saved from the perils of small number statistics by trusting a sample of the population over the noisy data from the environment. On the other hand, in a variable environment, the individuals one might learn from: (1) may have gotten caught in an environment switch, (2) might have migrated from nearby environment in the other state, carrying the wrong trait for their current environment, (3) might have mistakenly determined that the environment is in the state that it is not. If personal experience is sufficiently indicative of the state of the environment, it is liable to be the better guess. The optimal confidence rule (value of d) depends upon the nature of the environmental variation and the quality of the evidence available from personal experience. If the environment varies sufficiently rapidly in time or in space that individuals often find themselves in a patch different from their parents, individuals should depend entirely on their own experience. In such a world, parental behavior is a useless guide, and individuals should trust to the main chance of personal experience. As the statistical resemblance between parental generation and offspring generation increases, individuals should depend more upon social learning and demand ever more definitive personal evidence before breaking with tradition. In a world where the environment rarely changes between generations, but is rather noisy from the individual perspective, social learning becomes relatively trustworthy (Figure 2) and individuals should rely on a combination of natural selection and rather conservative reliance on own experience.

The *quantitative character model* is similar in spirit and leads to a similar conclusion. It has one continuous character (frequency of foraging alone versus cooperatively) and a continuum of environments from wet to dry. In any given environment at any one point in time or space, there is an optimal mix of solitary and cooperative foraging. Bayesian considerations suggest that individuals should use a weighted average of social learning and own experience to determine how to behave. The optimal weighting parameter in this model behaves qualitatively just as d does in the discrete character model. When two models with rather different structure give the same result we have some confidence that the results are robust to differences of detail.

Models focused on learning and social learning alone neglect the possibility that using genes instead of social transmission to transmit the population's "memory" to the next generation will restrict the range of environments in which social learning is favored. We (1985, Chap. 4) used the quantitative model to run a mathematical tournament comparing the

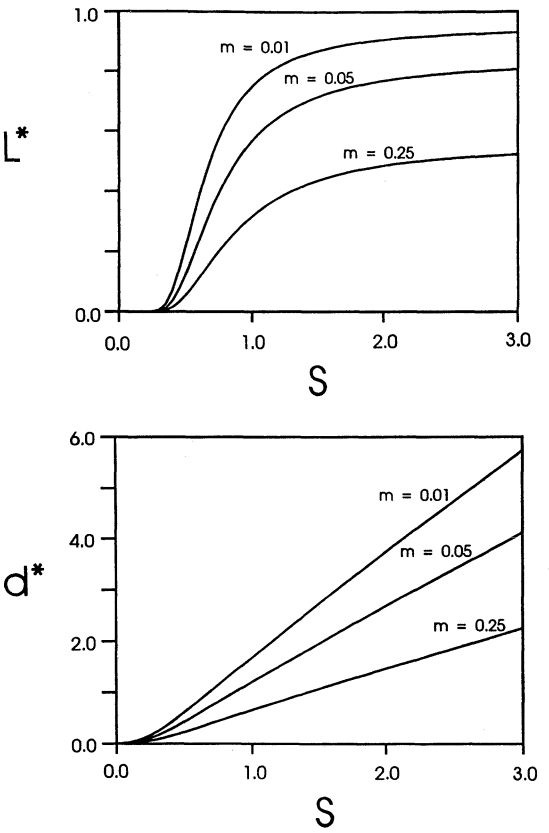

Figure 2. The values of d, the learning threshold and L, the fraction of young foragers acquiring their foraging mode by social learning, as a function of reliability of personal experience (S) and the amount environmental variability from generation to generation (m). The * indicate that these are the evolutionary equilibrium values of L and d, those that maximize fitness. Note that for environments that are harder to figure out (S large), the best thing to do is to rely more on social learning (d* and L* increase). Contrariwise, as the real change in the environment increases from generation to generation (m increases), it is best to trust more in own experience even at the risk happening to get the wrong answer by chance. (From Boyd and Richerson, 1989.) First published in Lectures on Mathematics in the Life Sciences, published by the American Mathematical Society.

fitness advantages of a conventional combination of genes and individual with learning a Lamarckian combination of social learning and individual learning. Suppose that there is some cost to being able to learn socially. Under what circumstances might selection favor adding social learning to the standard system where genes represent the wisdom of evolutionary

history and individual learning does the fine tuning? The analysis varied the degree of fluctuation of the environment and the autocorrelation between the environments of younger naïve learners and their potential teachers. If the variation is not autocorrelated at all, a statistical relationship between the environments of potential social learners and experienced individuals is absent. If the autocorrelation is very high, pace of environmental change is very slow; though the environment may vary in the long term, the change from generation to generation is quite modest.

A typical example of the results is shown in Figure 3. The social learning system has potential advantage over a wide range of conditions. The advantage of social learning is especially large when the environmental variance (V_H) is high and the degree of autocorrelation is high, but not too high. Under the parameter values chosen for illustration at least, the optimal dependence on social learning is often fairly high, on the order of a 75% dependence on social models and a 25% dependence on individual learning. At very high autocorrelations, environments become so slowly changing that genes can track perfectly well, and the advantage of social learning disappears. The model suggests that social learning should be common, at least among social species living in variable environments.

We studied several other models in which the rules of social learning are more sophisticated than the copying of a random member of the population (Boyd & Richerson, 1985: Chaps. 5–7). For example, a socially learning individual might use several adults as models. If they exhibit two or more behaviors, the social learner might try each out and retain the one most often rewarded. Most behaviors current in a population are probably better than the trials that individual learners can attempt on their own. Plagiarism is easier than originality. Gathering a number of plausible initial guesses about the right behavior and using one's own experience to choose the best among them has advantages similar to the guided variation process discussed above. We call the series of forces on cultural evolution that result from non-random social learning "biased transmission."

Humans and some other animals also use cultural systems to evolve symbolically marked boundaries between sub-populations. This subdivision permits adaptive specializations to narrow niches to evolve rapidly. Much like speciation isolates ancestral populations by shutting off gene flow between them, culturally isolated groups reduce the flow of extraneous ideas from other environments so that their local adaptations can be perfected. Ethnic groups are a common example. Often, such groups are specialized to exploit particular habitats or economic roles (Barth, 1969). Models show that cultural badges—different language, dress, religious practices—can evolve to erect barriers to the free flow of ideas in spatially

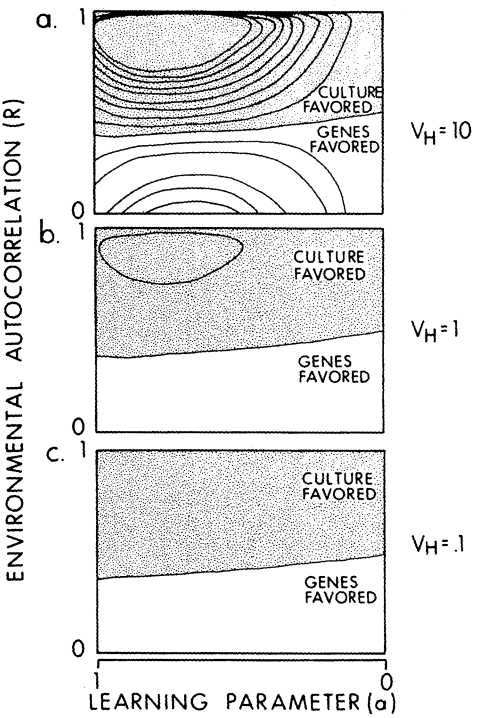

Figure 3. Contour plot of the differences in the fitness of populations using culture or social learning versus genetic transmission to convey information from the older to the younger generation. Both populations use the same individual learning rule, the only difference is that the cultural population has the inheritance of acquired variation so that both learning and natural selection drive behavior in an adaptive direction. The cultural system is assumed also to have a higher random error rate. Here (a) measures the amount of social learning, R the environmental autocorrelation (the degree to which offsprings' environments resemble those of their parents), and V_H the amplitude of the environmental variation. The exact shape of the topography depends upon variables not pictured here, but the qualitative results hold for a wide range of those parameters. Cultural transmission is favored whenever the resemblance of parental to offspring environments is sufficiently high. It is especially favored when the environmental change is quite large but fairly slow on the generational time scale. In the situation where the advantage of the cultural system is maximal, the dependence on social learning is substantial, around a = 0.75. Note that if R gets large enough, genes win again because in a stable environment the higher "mutation" rate of social learning favors the more exact system of transmission. (From Boyd and Richerson, 1985: 127.) Copyright © 1985 by the University of Chicago.

heterogeneous environments (Boyd & Richerson, 1987). (This is not the only evolutionary consequence of symbolic cultural badges, see Boyd & Richerson, 1985: Ch. 8.) Ethnic groups thus form the cultural analogs of reproductively isolated species. The main difference is that the barriers are much more permeable and the rate of evolution of culture is much higher than that of genes. Human cultural niche shifting is faster than that of animals that adapt mainly by organic evolution. Using this "psuedo-speciation" mechanism, late Pleistocene humans developed such a diverse array of subsistence economies that our species spread to the ends of the habitable earth (Bettinger, 1991, p. 203–5). Humans may not be the only species that uses this mechanism. Many birds learn their songs by imitating adults, creating local song traditions. Females may prefer to mate with males that sing the songs their fathers sang, potentially allowing the frequency of locally adapted genes to increase by restricting gene flow between groups (Nottebohm, 1975). Toothed whale vocalization dialects lead to similar population subdivisions according to Whitehead (1998).

The adaptationist account of non-human social learning is far from fully tested. An alternative hypothesis is that social learning has not come under selection for its improvement but is merely a byproduct of individual learning. Social learning may even be parasitical. Rogers (1989, see also Boyd & Richerson, 1995) constructed a model in which a social learning genotype could invade a population of individual learners. Initially, social learning is favored because social learners avoid the cost of individual learning and because they almost always imitate an individual learner. Thus, rare social learners get, on average, as adaptive a trait as they would get learning for themselves and they get it at less cost. However, as social learning increases in frequency, many social learners will acquire their behavior from another social learner. As the amount of individual learning declines, the reliability of social learning also declines. The social learners increase until their fitness falls to that of individual learners. Social learning in this case is not adaptive in the sense that it doesn't, in the end, raise the fitness of the individuals that do it. The reason that social learning is adaptive in the our models is that individuals in their model use a strategy that mixes individual and social learning such that social learning makes individual learning cheaper and more accurate. Lefebvre (in press) discusses the tendency of flock living birds to scrounge off the food-finding behavior of skilled flock members, acquiring new food strategies by social learning without any apparent efforts to learn individually. The fitness consequences of social learning are yet to be measured in any species. Cases fitting Rogers' model are likely to turn up, and may be common.

The theoretical models thus provide only tentative "in principle" support for the hypothesis that a capacity for social learning is likely to be

favored by variability selection. Do the paleoenvironmental and paleontological records give any empirical support to the hypothesis?

3. PLEISTOCENE CLIMATE DETERIORATION

The first element of the empirical test of the hypothesis is whether the Earth's climate has imposed a regime of variability selection on humans and other lineages using social learning as a means of adaptation. The critical period for the evolution of human brains and origin of complex culture is the late Pliocene and Pleistocene geological epochs (hereafter "Pleistocene" for short), about the last 3 million years (Klein, 1999). As we will see in the next section, many mammalian lineages probably evolved more sophisticated capacities for learning and social learning during the same period. Do climates of the recent geological past exhibit a pattern of increased variability with patterns of autocorrelation that might favor the evolution of capacities for social learning in accord with the predictions of the models?

Using a variety of proxy measures of past temperature, rainfall, ice volume, and the like, mostly from cores of ocean sediments, lake sediments, and ice caps, paleoclimatologists have constructed an increasingly detailed picture of climate deterioration over the last few million years, culminating in the Pleistocene ice ages (Bradley, 1999). The trend of deteriorating climates began in the mid-Miocene, about 14 million years ago. By the Pleistocene, the Earth's temperature had dropped several degrees and the amplitude of climate variation increased nearly 10 fold (Figure 4). The earliest fossils of the genus *Homo* and the first stone tools appear about 2.5 million years ago, at the end of the late Pliocene deterioration episode when the climate underwent a marked cooling and increase in the amplitude of fluctuations. The onset of the classic expansions and contractions of Northern Hemisphere continental ice sheets began in the middle Pleistocene about 900,000 years ago. Minimum temperatures at the height of glaciations became colder still and the amplitude of fluctuations increased still further. The final modernization of human anatomy and many aspects of culture occurred in the last 100,000 years. The origins of agriculture, and complex, literate societies date only to the last few thousand years, following a dramatic Holocene amelioration of the climate (Figure 5).

Pleistocene environments varied greatly in complex ways that presented organisms with major adaptive challenges. Many environmental variables were entrained in the Pleistocene glacial fluctuations. For example, glacial environments were not only colder but drier and had lower

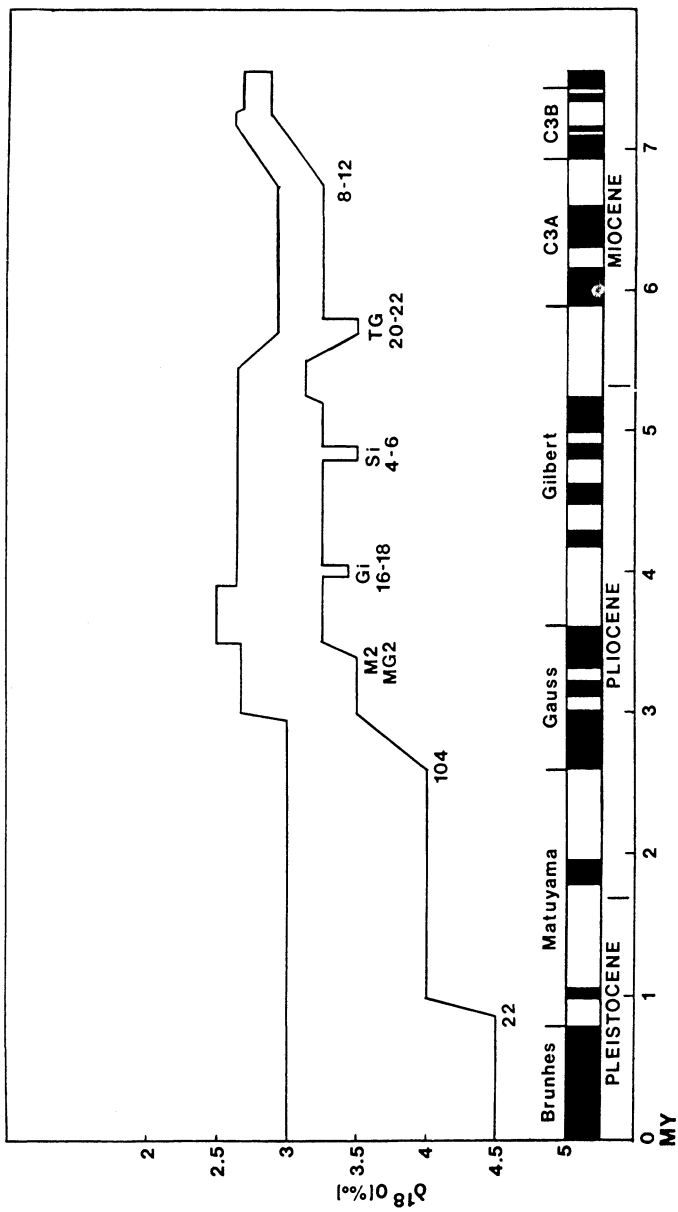

Figure 4. The envelope of variations in the oxygen isotope record for the last 7 million years in marine sediments. The oxygen isotope record, based on samples of foraminiferan shells, is a proxy measure of volume of ice locked up in continental glaciers. Greater concentrations of the heavy ^{18}O isotope indicate cold, high ice conditions. Thus, the climate over the last 7 million years has gotten cooler on average and very much more variable. A significant increase in variability occurred just after 6 million years ago, and again in the middle Pliocene. Another sharp deterioration occurred in the middle Pleistocene. (From Opdyke, 1995.) Copyright © 1995 by Yale University.

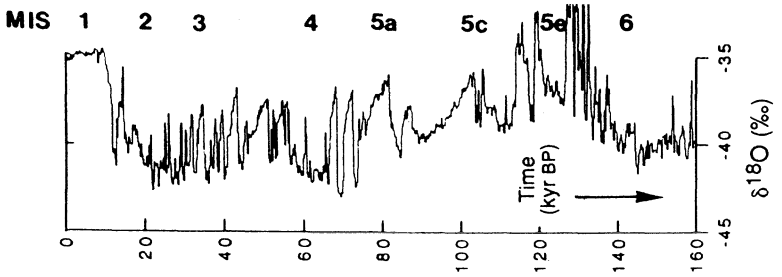

Figure 5. The oxygen isotope paleoclimate proxy from the Greenland Ice Core Project core drilled nearly 3,000 m to bedrock on a nearly stationary part of the Greenland ice cap. Ice depleted in the heavy isotope of oxygen (more negative values) indicates that large volumes of fresh water, depleted in ^{18}O, are stored in the continental glaciers. Note the very sharp peaks and troughs during the last cold period (Marine Isotope Stages 2–4). These are the Dansgaard-Oeschger and Heinrich fluctuations. The replicate GISP2 core agrees remarkably well with the GRIP core back to MIS 5c. The deeper part of the record, MIS 5e and 6, may be disturbed by ice flow (Grootes et al., 1993). Note that the last 10,000 years have been very much less variable that the other parts of the record. Reprinted with permission from Nature, GRIP (1973), copyright © 1993 Macmillan Magazines Limited.

CO_2 content (deMenocal, 1995; Raynaud et al., 1993). Thus, during glacials overall plant productivity was lower, but a higher percentage of plant communities were tundra, shrub desert, and steppe, which favor large herbivores. Ocean currents shifted dramatically (Lehman, 1993). The causes of the Pleistocene climate deterioration are not well understood. They are probably the result of basic geological processes, such as the isolation of the Antarctic continent from warm ocean currents by circum-Antarctic currents flowing through the gap created by continental drift between Antarctica and South America (Partridge et al., 1995).

As time series analysts say, the climate record of the past few million years is highly non-stationary. Not only does the climate vary, but also the statistics that describe the variation—the mean, variance and patterns of autocorrelation—change with time. The amplitude of fluctuations in temperature (and many other climate variables) increased as mean temperature dropped, as Figure 4 shows. The pattern of fluctuation in climate is very complex. Much of the variation seems to arise from an enhanced sensitivity to radiation changes caused by periodic variations in the Earth's orbit and its orientation with respect to the sun. The radiation income in high northern latitudes has a 20% range of variation due to these effects (Milankovitch, 1941; Broecker & Denton, 1990). The eccentricity of the Earth's orbit varies on a 95,800 year time scale, the inclination of its axis with a periodicity of 41,000 years, and the precession of the equinoxes with a periodicity of 21,700 years. As the deterioration has proceeded, different

cycles have dominated the pattern, causing different patterns of autocorrelation. The 21,700 year cycle dominated during most of the Pliocene, the 41,000 year cycle between about 3 and 1 million years ago, and the 95,800 year cycle from 1 million years ago to the present (de Menocal & Bloemendal, 1995). These shifts in dominant frequency correspond to the step-like increases in amplitude of the fluctuations illustrated in Figure 4.

More significant for the ecological processes that drive evolution, the rather stately fluctuations on the time scale of the orbital cycles have a great deal of rapid, noisy fluctuation superimposed on them. On the time scale of 10s of thousands of years, the environment is probably so highly autocorrelated on the generation-by-generation time scale that organic evolution and migration can track changes well enough. For the last 120,000 years, data from ice cores taken from the deep ice sheets of Greenland and Antarctica document a great deal of variation on much shorter time scales (GRIP, 1993; Lehman, 1993), as can be seen in Figure 5. The time resolution in these cores is as high as a decade even deep in the cores. Even when the climate is in the grip of the ice, there were brief excursions of about a thousand years' duration in which the climate reached near interglacial warmth. The largest of these warm spikes caused mass wastage of the continental glaciers, detected as layers of coarse iceberg-rafted erosion debris in ocean sediment cores (Lehman, 1993). Data from the upper part of the Greenland ice cores shows that the last glacial was considerably more variable than the last 10,000 years on time scales of a few years, the minimum that can be resolved due to diffusion mixing the cores. Presumably, the greater variability extends right down to the degree of variation between years (Ditlevsen et al., 1996). The Pleistocene climate appears to have ample variance at many different time scales to drive selection for mechanisms to adapt to it. No matter what generation length we consider, much variation is likely to have existed with degrees of autocorrelation that would favor social learning.

The causes of the high frequency variation in the Greenland ice data are uncertain, but most likely involve interactions of ice, atmosphere, and ocean current dynamics that are thrown out of equilibrium by the longer time scale processes and by the unstable dynamics of ice sheets (Broecker et al., 1985; Manabe & Stouffer, 1995; Cane, 1998). The last Interglacial (65,000–130,000 years before present) may also have been highly variable on the short time scales, as it seems to be the case in Figure 5. Interpretation of the deeper portions of the Greenland ice cores is controversial because of the possibility that ice from colder and warmer periods has been folded by ice movement to create false fluctuations (Grootes et al., 1993). Nevertheless, many lower-resolution records of the last interglacial also suggest that it was frequently punctuated by episodes of near-glacial cold (e.g., Lamb, 1977: 333). Significant stretches of warm, moist, relatively

invariant climate were probably quite unusual in the Pleistocene. A recent long core from Antarctica shows that the previous 3 interglacials were mere spikes of warmth compared to the 11,000 year long plateau of the Holocene (Petit et al., 1999). The possibility that our current climate system might be easily tipped into a regime of much greater variability by relatively weak forces is cause for considerable worry regarding human caused increases in carbon dioxide and other greenhouse gasses (Broecker, 1997).

Our picture of the high frequency variation of the Pleistocene climate system is incomplete. It is a reasonable inference that pre-Pleistocene climates were much like the last 11,000 years, and that the current tranquil period is unusual for the Pleistocene. It is a reasonable inference that the extreme climate variations at the generation-to-generation time scales that are recorded in the ice cores dating to the last glacial are typical of the whole Pleistocene but not of earlier Epochs. These inferences can be tested. Paleoclimatic records are far from fully exploited. For example, the African Great Lakes, especially Lake Tanganyika, have sediment columns several million years old that have yet to be cored. Sediments from lakes or ocean basins with anoxic bottom water are barren of invertebrates that stir ordinary sediments and hence can have records as good as ice cores, but with less distortion and mixing with depth (Behl & Kennett, 1996).

4. BRAIN SIZE EVOLUTION IN THE PLEISTOCENE

Mammals show clear signs of responding to Pleistocene variability selection with Potts' hypothesized increased behavioral flexibility. Harry Jerison's (1973) classic treatment of the evolution of brain size (relative to body size) documented a major trend towards increasing brain size in many mammalian lineages that persists right up to the present. Figure 6 summarizes his data. The data are presented in the form of cumulative frequency distributions of encephalization quotients of carnivores and ungulates over the whole Cenozoic Era. The sample includes:

(1) archaic creodont carnivores (an extinct order),

(2) archaic ungulates and carnivores from the extinct orders Condylartha and Amblypoda from the Paleogene (65–22.5 million yrs before present),

(3) members of the still extant ungulate and carnivore orders from the Neogene (22.5–2.5 million years before present), and

(4) a selection of living species of ungulates and carnivores.

The time trends illustrated by the figure are complex. There is a progressive increase in average encephalization throughout the Cenozoic.

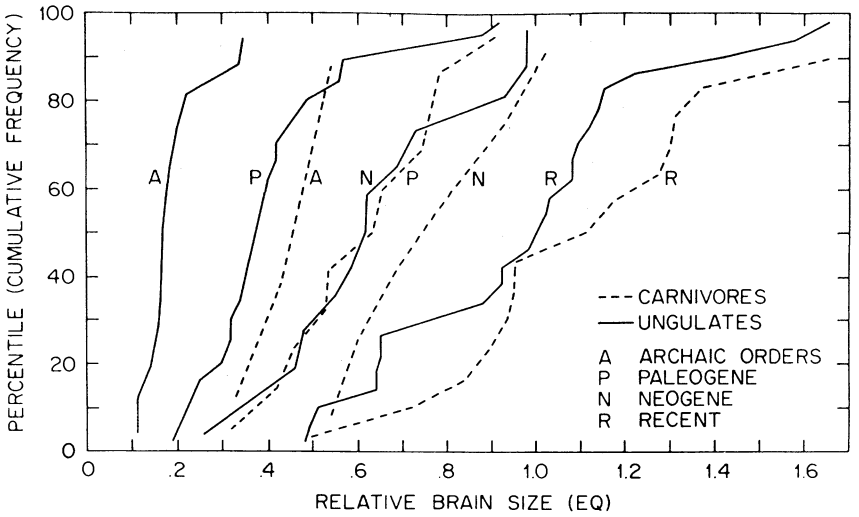

Figure 6. Cumulative frequency distributions of encephalization quotients in fossil and Recent ungulates and carnivores. Encephalization coefficients measure brain size corrected for body weight. (From Jerison 1973: 311.) Copyright © 1973 Academic Press.

However, many relatively small-brained mammals persist to the present even in orders where some species have gotten rather large brains. The diversity of brain size increases toward the present. Why might variability selection have resulted in this pattern rather than an increase in brain size in all mammalian lineages?

There is good reason to expect that, all-else-equal, selection favors as small a brain as possible. Sophisticated learning systems require larger sensory and nervous systems than simpler ones. The incremental energetic costs of maintaining this extra nervous tissue are quite large (Eisenberg, 1981, pp. 235–6). Mammalian brains vary over about a 25-fold range, controlling for body size (Martin, 1981). Human brains are about 5 times as large as the brains of average mammals of our body weight. Living ungulates and carnivores have average brains. Average living mammals in turn have brains about 5 times as large as those of the smallest brained mammals, such as insectivores and many marsupials. Human brains account for 16% of our basal metabolism (Aiello & Wheeler, 1995). Thus average mammals will have to allocate only about 3% of basal metabolism to their brains, and some get by with less than 1%. Total metabolism runs about 1.8 times that of resting metabolism, mostly because of the mobilization of large masses of otherwise low-metabolic-rate skeletal muscle during exercise. How nervous system metabolic rate varies with "exercise" is poorly

understood. Even disregarding mental exercise, humans must expend something like 9% of their total metabolism on their brain versus a little more than 1% for average animals and well under 1% for the least brainy mammals. Other costs of big brains, such as increased difficulty at birth and greater vulnerability to head trauma, are no doubt appreciable as well.

Since the fitness costs of large brains are significant, mammals continue to be under strong selection pressure to minimize brain size, and those that find an effective way to cope with climatic deterioration by non-cognitive means will do so. For example, many creatures like opossums cope with high mortality when times are bad by producing large numbers of small-brained offspring when times are good. It is thus not surprising that many mammalian lineages have undergone minimal encephalization despite a great increase in environmental variability. Other lineages evolve larger brains that allow them to exploit the temporal and spatial variability of the environment by using behavioral flexibility instead. Big-brained lineages pay for the cost of encephalization by exploiting the ephemeral niches that species with other responses to variability selection leave underexploited.

Humans merely anchor the tail of the recently much-stretched distribution of brain sizes in mammals. We are the largest brained member of one of the largest brained mammalian orders (Marino, 1996). The continuum of brain sizes is comforting to a Darwinian hypothesis. Large gaps between species are hard to account for by the processes of organic evolution. That we are part of a larger trend suggests that a large scale, general selective process such as variability selection is really operating.

Note that biggest shift per unit time by far is the shift from Neogene to the present. In the 2.5 million years from the late Pliocene to the end of the Pleistocene, encephalization increases were somewhat larger than the steps from Archaic to Paleogene and Paleogene to Neogene, each of which represent tens of millions of years of evolution. Thus, the increase of brain size did closely shadow the Pleistocene climate deterioration, although the precision of the correlation is limited by the low resolution of the brain size data.

Nevertheless, the Pleistocene leap in brain size is part of a trend that reaches back before the beginning of the Cenozoic. Since reasonably detailed records of climatic variability are so far only published for the last 6–7 million years (Figure 4), we cannot say whether a record of climate deterioration, especially high frequency variation, accompanies the earlier increases in encephalization. If Pleistocene increases in variability drove encephalization during the recent past, then the modest increases in encephalization in the early and middle Cenozoic were likely the product of earlier modest climate deterioration. To test this sub-hypothesis we need data on climate fluctuations on fairly short time scales. The analysis of

fossilized lake sediments with distinct annual deposition layers might put this part of the hypothesis to the test.

5. LARGE BRAINS FOR WHAT?

Increases in brain size could signal adaptation to variable environments via enhanced individual learning, for example through the addition of more innate information about the environment, or the addition of the psychological mechanisms that allow social learning. The mathematical models suggest that that the individual and social learning work together. Innate rules are necessary to make adaptive decisions in the processes of individual learning and biased transmission. There should be an optimal balance dictated by the spatio-temporal structure of the variability selection imposed upon a species, taking into account how the species niche "filters" raw environmental variation. Given the tight constraints imposed on brains, we would expect to find a tradeoff between social and individual learning abilities. Those species that exploit the most variable niches should emphasize individual learning while those that live in more highly autocorrelated environments should devote more of their nervous systems to social learning. The degree to which innate rules should tightly constrain and bias individual and social learning versus evolving more open, riskier, learning heuristics depends upon the degree to which selection can "detect" predictable patterns of variation in the environment versus the quality of heuristics available for responding appropriately to less predictable variation.

The relationship between individual and social learning has been studied most extensively in birds. Lefebvre (in press) reviews the experimental evidence from a variety of species and reports on a study of feeding innovation rates as observed by field ornithologists. For the most part, the patterns found do not support the hypothesis that individual and social learning are alternative specializations. Both forms of learning tend to be correlated with low neophobia (a low latency to feed on new foods or in a new apparatus), large forebrain size, and opportunistic invasion of new habitats, such as cities. Lefebvre interprets the data to support the hypothesis that large brains in birds usually signal a general-purpose opportunistic resource acquisition strategy using more individual *and* more social learning than the more specialized strategies of smaller brained birds. The former are often social, flocking birds, and the latter are generally territorial and less social. Interestingly, exceptions to the generalization exist. Caching species in the corvids and parids have extraordinary spatial learning abilities associated with enlargements of the hippocampus. However,

these abilities are not reflected in improved social learning. Birds include species, such as parrots, with extraordinary imitative abilities (Moore, 1996). Comparative work with birds promises to be one of the most interesting fields for testing general hypotheses about learning and social learning, and their relationship to the innate cognitive structures.

Why might individual learning and social learning be positively rather than negatively correlated? Individual and social learning may not be strongly competing processes and might even be synergistic. Jerison (1973) argued that the expansion of the neocortex, which accounts for most of the tissue involved in encephalization trends, is devoted to "maps" of the environment. Animals with more detailed maps need to acquire the information to fill them out. Both social and individual learning will help do so. Perhaps the information-evaluating neural circuits used in social and individual learning are also substantially shared. Once animals become social, the potential for social learning arises. If the two systems share the overhead of maintaining the memory storage system and much of the machinery for evaluating the results of experience, the benefits in quality or rate of information gain may be increased by the opportunity for social learning, leading social learners to become better individual learners. If members of the social group tend to be kin, investments in individual learning may also be favored because sharing the results by social learning will increase inclusive fitness.

The hypothesis that the tradeoff between social and individual learning may be modest except at the margin resonates with the mechanisms of social learning found in best-studied cases of social learning. The most common forms of social learning result from very simple mechanisms that piggyback on individual learning (Galef, 1988, 1996; Laland et al., 1993; Heyes & Dawson, 1990). In social species, naïve animals follow more experienced parents, nestmates, or flock members as they traverse the environment. The experienced animals select highly non-random paths through the environment. They thus expose naïve individuals to a highly selected set of stimuli that form the basis for acquisition of behaviors by ordinary mechanisms of reinforcement. Social experiences act to speed up and make less random the individual learning process, perhaps requiring little additional, specialized, mental capacity. Social learning, by making individual learning more accurate without requiring much new neural machinery, tips the selective balance between the high cost of brain tissue and advantages of flexibility in favor of more flexibility. As the quality of information stored on a map increases, selection will favor larger scale maps to take advantage of that fact. Eventually, diminishing returns to map accuracy will limit brain size. At that point only, marginal tradeoffs between individual and social learning may begin to select for cognitive structures specialized for one versus the other.

Data on the encephalization of living mammals suggests that high encephalization is associated with longer times of association with parents, late sexual maturity, extreme iteroparity, and long potential life span (Eisenberg, 1981, Ch. 23). These life cycle attributes all make social learning easier and hence more likely. Perhaps the opportunity to learn socially from parents allows investments in larger brains necessary for social learning to be amortized over a long life. Even marginally social species may come under selection for behaviors that enhance social learning, as in the well known case of mother housecats to bring partially disabled prey to their kittens for practice of killing behavior (Caro & Hauser, 1992).

If the relationship between social and individual learning is as tight as this evidence suggests, then we can expect to find social learning in many if not most social species, given that individual learning is so common. Indeed, the food choice system of Norway rats is the best studied example of non-human social learning (Galef, 1996). This species, with an encephalization quotient (brain size relative to body size) of about 0.4, is among those that have participated only modestly in the Cenozoic encephalization trend (Jerison, 1973, pp. 212 & 218). Average living mammals have a quotient of 1, whereas humans reach about 7.5. Social learning has been more or less convincingly demonstrated in a long list of animal species (Lefebvre & Palameta, 1988), including recently in guppies (Dugatkin, 1996; Laland & Williams, 1998). Social learning need not automatically favor large brains; in species where the costs of large brains are high relative to the benefits of more accurate maps, brains will remain small even if some social learning occurs.

Aspects of the social learning system in animals do show signs of adaptive specialization. For example, laboratory studies of black rats show that the main mode of social learning is from mother to pups (Terkel, 1996; Chou, 1989, personal communication). Norway rats' social learning is quite different (Galef, 1988, 1996). Mothers have no special influence on pups in this species. In the black rat, socially learned behaviors seem to be fixed after a juvenile learning period, whereas Norway rats continually update their diet preferences (the best-studied trait) based upon individually acquired and social cues. Black rats seem to be adapted to more slowly changing and Norway rats more rapidly changing environments. Terkel studied a rat population that has adapted an exotic pine plantation in Israel by the social transmission of the trick to efficiently extract seeds from the tough pinecones, a novel and short-lived niche by most standards, but one that will persist for many rat generations. Norway rats are the classic rats of garbage dumps, where the sorts of foods available change on a weekly basis. Interestingly, in recent decades, Norway rats have been expanding at the expense of black rats (Bentley, 1964). It seems possible that modern garbage dumps present a much more varied resource for rats than traditional ones, and that the spread of Norway rats reflects their better

adaptation to human modernity. The theory described here suggests that selection on social learners should tune the social learning system to match the statistical properties of the environmental variation in the specific niche the animal occupies. This very thin bit of data suggests that the hypothesis is worth pursuing.

In the human case, we have at least one highly specialized social learning system, language. On the other hand, we readily learn to make a living using a spectacular array of techniques. As the famous language learnability argument of Chomsky showed, a completely general learning machine cannot work (Pinker, 1994, Ch. 9). A finite learner must have a nervous system that in effect makes many "assumptions" about the environment in order even make the most basic map of its environment. For example, primates have a visual system imposes order on nerve impulses coming from the rods and cones to produce a fairly veridical image of objects in the world (Spelke, 1990). The flood of impulses arriving from a large array of sensory cells would overwhelm the capacity of a very general learning mechanism. A functional learning device requires built in expectations about what sorts of objects are out there to sense. For example, the visual system assumes that a set of spatially contiguous points in the visual field that have a similar color, a defined border, and coherent movement is a solid object. This innate physics correctly recognizes a rolling ball as a solid object, though it misidentifies clouds as such. On the other hand, the adaptive reason to have learning and social learning is the flexibility to adapt to unforeseen contingencies. Experience teaches us that the solidity of clouds is an illusion.

The idea that brain size, social learning and individual learning are an adaptive package serving as a rather generalized environment mapping system seems contrary to the attractive, widely held, idea that minds are collections of highly specialized, innate modules (Fodor, 1983). Innatist evolutionary psychologists argue that modular specialization of cognition is to be expected on general theoretical grounds (Tooby & Cosmides, 1989), and that the nature of the modules can be deduced from the nature of the adaptations they support. The positive correlation between capacities for individual and social learning in birds is perhaps more congenial to the connectionist hypothesis. Connectionists hold that much brain tissue functions as a rather generalized pattern recognition device. A major complexity arises in this debate because, as Fodor insists, different levels of organization have to be kept straight. The structure of the mind may not mimic the structure of its neural machinery. The same is likely to be true of adaptations compared to cognitive structures. Typical adaptations (e.g., ability to capture a certain class of prey) at the phenotypic level integrate many elements of anatomy and physiology. Many of the elements subserving one adaptation also subserve others (e.g., fighting abilities used in dominance struggles and to subdue prey). The same is likely to be true of cognitive structures relative to behavioral adaptations. Relatively general

purpose learning and social learning systems could well be based on the operation of a number of rather specialized modules at the cognitive level which in turn are built upon the rather general properties of neural nets at the brain tissue level.

Progress on these questions is limited because we know very little about the adaptive tradeoffs in brain and mind design (Richerson & Boyd, in press; for an introduction to what we do know see Allman, 1999, Chap. 7). We would like to build models in which the individual level synergies and tradeoffs between various forms of individual learning and social learning are included alongside the population level tradeoffs heretofore incorporated into them. How much brain space and energy do the various modes of adaptation to variable environments take? It is not yet possible to answer such questions. Neurophysiologists, cognitive scientists, and behavioral ecologists each have something to contribute to the puzzle of how some species can support large brains. Much will depend upon rather general considerations of neurophysiological, cognitive, and adaptive constraints and tradeoffs. Much is also likely to depend upon the details how mammalian brains, if not primate or hominid brains, are constrained by their evolutionary history. However, collaborations between these disciplines to tackle this question have been lacking. Until these tradeoffs are better understood, the support for the social learning hypothesis afforded by the correlation of brain size increase with climatic deterioration is suggestive but certainly not conclusive. The behavioral evidence does suggest that increased social learning was at least one component of the response to Pleistocene variability selection and one component of the cognitive adaptations supporting larger brains.

Perhaps the neocortex of the brain is an adaptation like the beak of birds. The basic beak is nothing more than a moderately complex, functionally integrated, general-purpose forceps-like device. It is usually a food acquisition, handling, and processing organ, fighting weapon, nest building implement, environment probe, and grooming tool, all in one. Nevertheless, despite great commonality of form and function, bird beaks are endlessly stretched, bent, thickened, widened, deepened, and sharpened by selection to support the diverse niches birds occupy. Only occasionally are entirely new parts, like the pouch of pelicans, added to create a new adaptation. The modularity-connectionist debate does not exhaust the possible models for the relationship between form and function in brains (Krubitzer, 1995).

6. HUMAN CULTURE IS DERIVED

The human species position at the tail of the distribution of late Cenozoic encephalization admits of the hypothesis that our system of social

learning is merely a hypertrophied version of a common animal system. However, the evidence suggests that human culture is qualitatively different from most, if not all, animal social learning systems.

Human culture differs from that of other species because it involves the assembly of very complex traditions over extended periods of time. Subsistence systems, artistic productions, ideologies, and the like are so multiparted and intricately integrated that no one individual ever could or did invent them. Nor, merely given the pieces and motivation to produce a complex artifact, would stimulus enhancement provide sufficient clues for a simple social learner to produce a workable version. Think of some relatively simple item like a hunting spear. The maker has to know how to make the stone tools to prepare the shaft, how to knap fine-grained stone to make a good point, how to prepare stout adhesives and fiber to mount the point, what wood makes a spear of the right strength and weight to be useful, how long and stout to make the shaft for the intended purpose (throwing, stabbing, atlatl dart, multipurpose), and so forth. Few of us could make more than a crude approximation of a Stone Age spear, though we could easily learn by being taught, or even just by observing an expert spear-maker. The knowledge of how to make such complex artifacts is built up over many generations by the incremental, marginal modifications of many innovators (e.g., Basalla, 1988). We are utterly dependent on learning such complex traditions to function normally. By contrast, most animal proto-culture involves simple behaviors that individuals can and do learn on their own. The study of the manner in which it roof rats open pine cones showed that individuals cannot normally learn to open a pine cone in a way that leads to a net energy gain (Terkel, 1996). However, rats need to learn only one trick to acquire the successful technique. A single individual presumably innovated the trait in the beginning.

The cumulative complexity of human culture appears to be based on an ability to acquire novel behaviors by observation, "true imitation" in the lexicon of comparative psychologists. As we saw above, much social learning seems to be dependent mostly on the same cognitive strategies used in individual learning. Experimental psychologists have devoted much effort to trying to settle the question of whether non-human animals can learn by true imitation or not (Galef, 1988). True imitation is learning a behavior by seeing it done. True imitation is presumably more complex cognitively that merely using conspecifics' behavior as a source of cues to stimuli that it might be interesting to experience. Some good experiments indicate a modest capacity for true imitation in many socially learning species (Heyes & Dawson, 1990; Moore, 1996; Zentall, 1996), but it seems to play a modest role in most cases of non-human social learning. Even our closest relatives show quite modest abilities to imitate. Head-to-head comparisons of children's and chimpanzee's abilities to imitate show that children begin to

exceed adult chimpanzees' capabilities at about 3 years of age (Tomasello, 1996; Tomasello & Call, 1997, Chap. 9; Whiten & Custance, 1996). Whether or not wild chimpanzees make much use of imitation is unclear. Tomasello is inclined to think that even in this species, there is remarkably little indication that apes can ape, although human reared chimpanzees do show considerable imitation or quasi-imitative "emulation." Whiten and Custance, on the other hand, argue that the marginal abilities observed under impoverished captive conditions are likely to underestimate abilities in the wild. Arguably, chimpanzee tools are as complex as the simplest know toolkits of humans, those of the Tasmanian Islanders (McGrew, 1992). Chimpanzees exhibit a few tens of traits that are plausibly cultural (Whiten et al., 1999). Perhaps some chimpanzee tools, especially the hammer-and-anvil nut cracking system found in some West African populations, is a cumulative tradition that is made up of at least two independent inventions, the hammer and then the anvil. Rehabilitated pet orangutans exhibit impressive, though still imperfect, imitations of complex human behavioral routines, such as kindling a fire. Orangutans are not known to have any sign of imitatively acquired behaviors in the wild (Russon & Galdikas, 1993). Parrots seem to have a quite respectable but little understood capacity for imitation (Moore, 1996). On the other hand, monkeys show scant signs of abilities to imitate. Even Capuchin monkeys, who have a higher encephalization quotient than even the great apes, fail imitation tasks (Eisenberg, 1981, p. 499; Fragaszy & Visalberghi, 1996). Thus, the lesson to date from comparative studies of social learning suggests that very simple mechanisms of social enhancement of cues are much more common than imitation, even in our close relatives and other highly encephalized species. Humans seem to be unique at least in the ease and wide range of behaviors with we can imitate, and in the scale and importance of our complex traditions.

The evidence that imitation is a major cognitive ability distinguishing us from other encephalized mammals, together with the evidence that we use imitation to support complex traditions, suggest that transmitted culture is a central, if not the central, problem for human evolutionary psychology. We are perhaps the only species that is sufficiently imitative to create complex traditions in the wild, but we do create them with abandon. Anthropologists have long argued on good grounds that complex, transmitted cultural traditions are central to the adaptations of hunter-gathers (e.g., Steward, 1955). How else are we to account for the dramatic variability in technology and social organization among hunter-gatherers or the dramatic historical changes in human behavior under the quiet environmental regime since the end of the Pleistocene? The innate "evoked culture" of Thornhill, Tooby, and Cosmides (1997) would equilibrate human behavior to changed circumstances in one generation, whereas cultural traditions exhibit descent with modification over many generations. The conventional

social sciences are no doubt guilty of neglecting innate attributes of human minds (Bateson, 1987), but neglecting complex cultural traditions is not progress.

7. WHY IS CUMULATIVE CULTURAL EVOLUTION RARE?

The hypertrophy of imitation and culture in humans generates the problem of a "great gap" in accounting for human minds by a Darwinian explanation. Humans have apparently penetrated a "cultural niche" that made us a rather successful species under Pleistocene conditions. The gradual cultural assembly of complex traditions allowed humans to occupy environments from the tropics to the glaciers, penetrating to all but the harshest environments. In the Holocene, the development of food plant production has made us the Earth's dominant organism. If human traditional culture is a successful adaptation for us, why haven't other species evolved similar capacities?

Perhaps the simplest answer is that we have simply won an evolutionary footrace to be the first animal to occupy the cultural niche. There may be only one cultural niche because the first animal to occupy it excludes all competitors by occupying so many niches using so many different traditional modes of subsistence. Perhaps any one of a number of highly encephalized primate, elephant, or porpoise lineages might have evolved complex culture if hominids had not gotten there first. Some key initial condition may have given our lineage the head start necessary to beat out all competitors. The classic explanation is that upright posture, freeing the hands to make and carry artifacts, was a preadaptation that made complex traditions especially useful (Tobias, 1981). If human evolution was the product of a single breakthrough, we might expect a smooth, rapid entry in the cultural niche and then a stabilization of the imitative adaptation while cultures varied dramatically in response to climatic variability.

The actual paleoanthropological record tells a very different story. The human lineage seems to have been on a progressive, but very complex, trajectory toward a heavy dependence on cumulative cultural including at least four major sequential improvements, the first manufacture of stone tools, presumably by *Homo habilis*, around 2.5 million years ago, the expansion of *Homo erectus/ergaster* out of Africa about 1 million years ago, the evolution of archaic but large brained populations by about 200,000 years ago, and the expansion of anatomically modern *H. sapiens* out of Africa around 50,000–60,000 years ago (Klein, 1999, Chaps. 5 & 6). The manufacture of stone tools seems to represent a substantial increase in social learning ability, probably including a significant increment in ability to imitate, over

that demonstrated in other living apes. The erectus expansion carried hominids to the temperate latitudes of Eurasia. Cultural traditions are a means of adapting to spatially as well as temporally variable environments. The *erectus* expansion gave humans a geographical range that is unusually large for any vertebrate and probably signals the acquisition of a considerable capacity for imitation. *Erectus* and succeeding populations used more sophisticated stone tools than *habilis* and used them to make rather sophisticated tools of wood and probably hide. Wooden throwing spears, weighted for accurate flight like modern javelins, have been recovered from an anaerobic deposit in Germany (Thieme, 1997). However, the rate of evolution of Lower Paleolithic artifacts and their degree of geographical differentiation were restricted compared to modern populations. Between the two invasions from Africa, considerable increases in brain size and artifact sophistication occurred, but cultural evolution was still rather slow and low in regional diversification. Anatomically Modern people made the same Middle Stone Age and Mousterian tool kits as anatomically archaic people for some tens of thousands of years. To judge from the durable artifacts even large-brained Moderns and Neanderthals were not taking full advantage of culture to exploit temporally ephemeral and spatially variable environments. Mitochondrial DNA evidence suggests that Neanderthals and moderns had about 400,000 years of independent evolutionary history (Krings et al., 1997). For a long time the two species apparently coexisted in Western Asia, physically quite different but culturally quite similar.

This coexistence ended when a cultural revolution, marked by the advent of more complex Late Paleolithic artifacts, apparently gave Moderns a decisive advantage. Nevertheless, Neanderthals in Europe are associated with the modern-appearing Châtelperronian industry, suggesting an ability to make more sophisticated artifacts, perhaps stimulated by contact with Late Paleolithic Moderns. The Anatomical Moderns that invaded Eurasia 50–60,000 years ago generated the Upper Paleolithic Transition in Europe, settled Australia for the first time (requiring tolerably sophisticated boats), and expanded their range into colder and more continental environments than Archaic humans could occupy. The number of artifact types recovered from the sites occupied by invading Moderns, the degree of formalization of types, and the degree of spatial and temporal differentiation of cultural traditions all increase dramatically. On the utilitarian side, Late Paleolithic Moderns were the first humans to make tools of bone, including needles, fish hooks, and spear throwers. They also made the first unequivocal art. They completely replaced relatively small brained late *erectus* populations in East Eurasia but also large brained forms such as Neanderthals in Western Eurasia. Data from the West indicates that invading populations maintained higher population densities, and higher density probably explains the rapid replacement of archaic populations, such as the

Neanderthals. These rather dramatic changes in culture suggest some final modernization of human cognition within the last 100,000 thousand years (Klein, 1999, pp. 511–572; Stringer & Gamble, 1993).

On the other hand, the apparent ability of Neanderthals to make Châtelperronian artifacts means that we cannot rule out the hypothesis that the advantages of the Late Paleolithic invaders was mainly cultural, not cognitive. In either case, the existence of seemingly punctuational events separated by a periods of slower modernization suggests either the penetration of the complex culture niche is inherently slow or rare concatenations of events are required to penetrate it or both. Conceivably, cultural innovations, such as more effective teaching techniques, might have been as important as genetic changes leading to a capacity to maintain complex traditions, either alone or as part of a coevolutionary sequence. For example, perhaps the invention of the spear-thrower led to the modernization of human physiques in Africa and to higher population densities that in turn could support conspicuously more complex cultures, all without any significant cognitive changes. Perhaps because the very robust Archaic populations were anatomically less suited than gracile Moderns to using spear throwers, they failed to compete successfully with the Modern invasion.

Theoretical models suggest the evolution of a capacity for complex cumulative traditions faces a bootstrap problem—a capacity for complex cumulative culture cannot increase when rare even if it would be quite adaptive once it became common (Boyd & Richerson, 1996). The mathematical result is quite intuitive. Suppose that to acquire a complex tradition, learners need efficient imitation skills. Suppose that efficient imitation requires considerable costly, or complex, cognitive machinery to support an imitation capacity. If so, there will be a coevolutionary failure of capacity for complex traditions to evolve. The capacity is a great fitness advantage, but only if there are cultural traditions to take advantage of. But, obviously, there cannot be complex traditions without the cognitive machinery necessary to support them. A rare individual with a mutation coding for an enlarged capacity to imitate will find no complex traditions to learn, and will be handicapped by an investment in nervous tissue that has no function. If it takes a number of generations for a complex tradition to evolve, the offspring of the initial mutant individual will be almost as handicapped as their parent. Worse, a quite large population of sophisticated imitators might still take a considerable length of time to evolve enough useful traditions to make the imitative capacity pay for itself. The hypothesis depends upon there being a certain lumpiness in the evolution of the mind. If even a small amount of imitation requires an expensive or complex bit of mental machinery, or if the initial step in the evolution of complex traditions does not result in particularly useful ones, then there will be no smooth evolutionary path from simple social learning to complex culture.

The failure of a capacity for complex cumulative culture to evolve when rare is an example of the sort of process that gives evolution its commonly contingent, historical character (Boyd & Richerson, 1992). Natural selection is often portrayed as causing populations to climb fitness peaks. There are numerous processes that cause fitness topographies to be rugged, like real mountain ranges. Because it maximizes only locally, natural selection will tend to get stuck on local peaks. Selection is like a blind mountain climber; it cannot "see" distant higher fitness peaks across valleys and instead just goes up the current hill. If a relatively abrupt environmental change occurs, the initial adaptations will tend to be globally sub-optimal, represented by the tops fitness knolls near the initial phenotypes of adapting populations, far from the more nearly globally optimal high peaks. The problem is well understood in the context of the engineering of complex systems (Kirkpatrick et al., 1983). Complex design problems typically have an extremely large number of possible solutions, including a huge number of locally optimal solutions ("best" in the sense that all small modifications of the design are worse). There are also typically quite a few nearly equivalent globally "best" solutions that are qualitatively different from each other. In the longer run, various kinds of historical happenstance cause populations to escape local optima and climb higher on the topography. The notion of preadaptation captures the idea that traits evolved for one function sometimes put populations at the foot of a slope leading to a quite different adaptation. Some populations thus find an indirect route, via preadaptations, up a complex topography that has left competitors stuck in the foothills. Other processes, such as genetic drift and the constant small-scale wiggling of the topography due to environmental variability, likewise allow populations to move to higher peaks. Given enough time, some population will reach one of the more or less equivalent near-global optima. If this picture applies to human evolution, we expect to find that the perfection of our rather novel cognitive adaptation to Pleistocene environments is slow, roundabout, and punctuated by rushes from lower local optima to higher ones.

Some evidence supports the hypothesis that the utility of having a capacity for learning complex traditions is constrained by the number of others who have the capacity. Among modern humans, the maintenance of complex traditions is not unproblematic. The Tasmanians' originally normally complex toolkit shrank in size and sophistication after their isolation from Australia by the Holocene rise in sea level. The loss probably resulted from a sort of cultural drift (Diamond, 1978). In a small population, complex skills will occasionally be lost by accident. With few people to invent and reinvent, and no possibility of reacquiring complex traditions by diffusion, the Tasmanians were helpless to prevent a gradual erosion of their more complex cultural traditions. Even given a capacity for complex traditions,

the number of participants in a cultural system may be critical to the complexity that can be maintained. A few rare, unsophisticated imitators could not possibly have maintained even marginally complex traditions if fully modern humans have trouble maintaining them if regional populations are too small. On a grander scale, cultural evolution in Eurasia has proceeded along the trajectory toward politically and technically more sophisticated societies faster than in Africa and the New World. The likely reasons are two (Diamond, 1997). First, Eurasia is the largest continent, thus encompassing more cultural evolutionary experiments than Africa and the New World. Second, it is extended in the east-west rather than north-south direction, connecting ecologically similar regions of the continent and facilitating the rapid diffusion of relevant innovations, including the re-diffusion of any that are lost in a given population. Thus, some direct evidence supports the hypothesis that cultural traditions of the complexity created by the last major modernization of the culture capacity could not have increased when rare. Plausibly, the earlier increases in the sophistication of culture were slowed by similar bootstrap problems. For example, perhaps imitation and complex traditions were first restricted to a narrow domain, say food acquisition. Each extension to a new domain, say to social organization, may have faced a similar problem of not being favored when rare.

The paleoanthropological record supports the idea that the evolution of human cognition and culture occurred on a complex fitness topography. The two invasions from Africa seem to mark two major increases in the sophistication of the cultural adaptation. The first is poorly dated, but could have been an evolutionary response to the beginning of the dominance of the 95,800 year Milankovich cycle in the climate record. The second is not associated with any known change in the pattern of climate change. The evolution of the rather diverse populations of archaic but increasingly large brained hominids between the first and second invasions occurs without any conspicuous change in the pattern of climate variation. A million or so years seems to have been spent slowly enlarging brains and increasing the sophistication of artifacts, leading to a rather sudden and late emergence of modern culture. Most likely, evolving human populations encountered a number of local optima and adaptive valleys of the useless-when-rare sort over the 2.5 million years after the first signs of minimal imitative capacities appeared in the archaeological record.

If multiple major impediments to the evolution of complex traditions existed, evolution must have traveled a round-about path to achieve get the frequency of the capacity high enough to begin to bring it under positive selection for its tradition-supporting function. The exact path that evolution took to reach modern culture capacities is probably vain to seek; disciplined speculation is often the best that evolutionary science has to offer. What sort of evolutionary situation might finesse the problem of imitation not

being adaptive when rare? The best-developed suggestion along these lines is that primate intelligence generally was originally an adaptation to manage a complex social life (Humphrey, 1976; Kummer et al., 1997; Whiten & Byrne, 1988). In primates generally there is a correlation between group size and the size of the neocortex relative to the rest of the brain (Dunbar, 1991). Perhaps in our lineage the complexities of managing the sexual division of labor or some similar social problem favored the evolution of abilities to understand the intentions of others, the rudiments of a generative language, or some similar preadaptation. Such a capacity might then incidentally make efficient imitation possible, launching the evolution of complex traditions that could drive the evolution of still more sophisticated imitation. This hypothesis might apply to the original stone tool revolution or to the later modernizations leading up to the range extensions out of Africa. Perhaps it underpins all three in one way or another.

The second invasion out of Africa is plausibly associated with the evolution of language. Language is an extraordinarily powerful device for encoding and transmitting cultural traditions. The productivity of language allows humans to express a huge number of ideas and link them in patterned arrays. According to one well-known hypothesis, modern skull anatomy is required to make room for a vocal apparatus capable of making the modern range of vowel sounds (Lieberman, 1984). Even otherwise advanced hominids like the Neanderthals may have had only limited speech. Highly specialized neurological structures are required to code and decode speech at the rates we normally converse (Friederici, 1996). Language is potentially an example of the failure of a capacity for imitation to evolve when rare. If a complex capacity to learn grammar, form words, and decode words is required for speech to be a significant improvement to silent mimicry in acquiring cultural traditions, then it also cannot increase when rare. With no language to learn, there is no advantage to a capacity to learn one.

Language is much used for social purposes (Thompson, 1995; Dunbar et al., 1995) and this use could be the key link in the origin of the capacity for complex traditions. Plausibly, small steps in the increase of communication complexity allowed the coevolution of a language capacity and a cultural linguistic system. Communication about who-did-what-to-whom-when-and-why is the sort of thing that is hard to communicate accurately without grammatical structure. Social actors often want to communicate information about social events that occur out of the presence of their hearer. Even a talented mime has trouble conveying such information. Even a marginal increase in competence may allow one to convey a bit more information about a social relationship. Finally, a fully generative language arose, with the capacity to encode an unlimited number of messages. Even if the original function of language was gossip about social relations, it is a

ready vehicle for transmitting complex traditions, starting with the language itself.

Donald's (1991) admirably well specified scenario for the origins of human cultural complexity involves a stage of sophisticated motor mimicry preceding and laying the neurological basis for language. Donald argues that quite complex behavior can be acquired by mimicry in the absence of language. 19th Century accounts of the abilities of deaf-mutes to acquire many sorts of useful economic and social skills without language suggest that they could easily learn to most non-linguistic skills, including most social graces, by observation, without any linguistic aids. Donald argues that *Homo erectus* had evolved the basic memetic capacity, which accords well the pattern of the first invasion of Eurasia by hominids. These populations could probably sustain complex traditions of resource exploitation that allowed them to occupy an unprecedented diversity of niches. Fine motor skills are neurologically closely related to linguistic skills, suggesting that mimetic capacities were the preadaptation for language. A possible objection to Donald's hypothesis is that it does not explain why utilitarian artifacts made by *erectus* and its immediate successors evolved so slowly and were so similar across wide areas. Modern people who acquire such traits as stone knapping and woodworking substantially by direct imitation imitate fine details of performances but also readily invent new variants, generating rapid evolution. Deaf-mute Moderns would seem to be capable of much more. Young children, whose imitative capacities might be models for *H. erectus*, play inventively and imaginatively with toys. Would not free mimicry lead to something approaching the innovativeness of modern people as regards those functional aspects of tool technology that are easy to mimic? Perhaps innate constraints on learning and social learning were still relatively strong in erectus and its immediate descendants. The large-brained archaic toolmakers, such as Neanderthals, made considerably more complex tools than *erectus*. Whether this increase in sophistication was gradual or more discontinuous is hard to say given a sparse and poorly dated record.

The dramatic increases in tool complexity in some parts of the world about 50–60,000 years ago postdate the anatomical modernization of skeletons by perhaps another 50,000 years. If we suppose that anatomical modernization reflects something like the modern ability to speak language, then what took the further 50,000 years before Moderns were able to make the more sophisticated tools that supported the second invasion from Africa? If Moderns 100,000 years ago had relatively modern language, the imitative sophistication in the linguistic mode did not yet spill visibly into artifact production. Perhaps learning to make archaic tools required a relatively primitive imitative capacity. Perhaps the manufacture of artifacts of the complexity made by large-brained Archaics was still innately

constrained in ways that the imitation of Moderns is not. The relative crudity and uniformity of archaic tools, even the Mousterian and Middle Stone Age tools made for tens of thousands of years by anatomical moderns, suggest that a relatively small number of techniques were inherited and that controlled innovation that might lead to cumulative complexity is rare or at least rarely imitated. The stereotypy of archaic tool traditions in time and space suggests a very conservative form of transmission, with strong innate elements or tightly controlled teaching by parents. Or perhaps, only the basic steps of toolmaking could be imitated, and much refinement of technique by individual learning was still necessary. In this way, function and raw material properties might have dictated final form to a much greater extent than was the case for Late Paleolithic artisans who could easily copy minute nuances, whether stylistic or functional, of each others' artifacts. The penultimate hominid population preceding fully modern humans might have been linguistically advanced but still retarded in their abilities to imitate in other domains.

The linguistic system, even if first modernized for social communication not cultural transmission, could have made more complex cultural traditions possible by making it easy to express, memorize, and teach cultural principles verbally. Once language became fully productive, talk would occasionally turn from band politics and sex to technology. In this way, elements of material culture that were initially complex in the oral mode of transmission may then have selected for more facile mimetic capabilities for those common learning tasks where a picture is worth a thousand words. Once complex non-linguistic cultural traditions began to be built by linguistic means, selection might favor devoting costly brain tissue to learning them more efficiently by imitation. Donald's (1991) evidence for a close neurological relationship between language and mimicry is silent as to which came first. Perhaps a back-and-forth coevolution between mimicry and language was involved. We are used to thinking that language is the ultimate human cultural achievement. The evidence that much of the complexity of language is innate (Pinker, 1994) suggests that this system is actually more primitive than other cultural systems that appear to have a much smaller innate component, such as late Pleistocene and Holocene technology. If children have enough innate information to create a new language in one generation (Bickerton, 1984), this system may not really depend upon the existence of complex traditions, although it produces them as a byproduct. Perhaps modern motor mimicry abilities postdate the evolution of modern linguistic skills.

Of course, these scenarios, like any number of others that imaginative scholars can produce, are exceedingly difficult to test given the quality of the archaeological record. We can recover relatively little information about past behavior and past environments from the paleoanthropological record.

If the notion that the evolution of our capacity for cumulative culture was a complex design problem is correct, *Homo* might have taken any of a number of paths through the complex topography to reach the present state of human culture capacities. If the possible pathways are many and the historical data sparse, we will never be able to rule out a considerable number of alternative evolutionary trajectory our species might have taken. Likewise, predicting the details of modern cognitive capabilities by considering the adaptive function of cognition in the Pleistocene will be difficult. The more complex the fitness topography, the more unpredictable evolution becomes. We know from the commonness of analogous adaptations (the wings of birds, bats, insects, and airplanes) that many different structures may serve the same adaptive function. Selection puts constraints on the evolution of adaptations, but when there are many alternative evolutionary outcomes, these constraints are often not sufficient to predict the details of how the machinery will be organized. At the level of cognitive details, there are probably many more or less equivalent ways to make a mind capable of complex culture and the other things modern humans do. Even at the gross functional level the evolution of *Homo* is very puzzling. Archaic populations lacked something that prevented rapid innovations to adapt to local environmental circumstances. On the other hand, the artifacts that they did make are often quite impressive, especially compared to what other apes produce. Moderns would certainly well exercise their good imitation skills to learn how to make them, but would have a hard time not using these same skills to launch a trajectory leading quite shortly to much fancier things. Late Archaics had brains as large as ours, but apparently used them quite differently. How differently is highly uncertain. If this complexity tells us anything it tells us that past hominids are not just simpler versions of ourselves. They seem to have had quite different mixtures of capabilities and constraints than moderns do.

Evidence from human paleodemography suggests that some sort of rare evolutionary accident led to the final modernization of human culture capacities, as dated by appearance of modern artifacts during the last glacial. Human mitochondrial DNA records evidence of a human population explosion of the modern human lineage between 33,000 and 150,000 years ago (Rogers & Harpending, 1992). In small populations, genetic drift limits the diversity of mitochondrial genomes in the population. The age of diversification of mitochondrial DNA lineages can be estimated from the number of mismatches separating different lineages. If a small population rapidly expands, a large number of new mitochondrial lineages will arise more or less simultaneously and will be preserved against loss by drift. As these lineages accumulate more mismatches over time they generate a clock that allows us to estimate the time of the original population explosion. Although confidence intervals are wide, the data suggest that the

population ancestral to all modern humans was quite small around 60,000 years ago, when it began to expand rapidly. The pre-expansion population was between 1,000 and 7,000 breeding females for an extended period, although exactly how long is unclear. At the time of the final modernization of the human mind, we were most likely a rare and, given the nature of the Pleistocene, endangered species. Our numbers were probably much smaller than those of the archaic populations that we replaced after the explosion. The date of the explosion is consistent with the dates of the appearance of more sophisticated tools in Europe. Similar considerations apply to other genetic elements (Harpending et al., 1998). If critical events happened in a small population traversing a rugged fitness topography, recovering evidence about the exact evolutionary process led to our final modernization is likely to prove most difficult. If our lineage had gone extinct, who knows how many more glacial cycles would have passed with big-brained hominids poised on the threshold of the complex culture adaptation without crossing it?

The contribution of psychology to the study of human evolution is likely to prove to be at least as great as the contribution of evolutionary studies to psychology. The social psychology of living humans is available for study, while the behavior of our long dead ancestors is heavily veiled. The ability of clever experimentalists to dissect the function of organisms with only a little help from evolutionary theory is well illustrated by physiology, cell biology, and molecular biology. Evolutionary biologists have turned all of these sciences to good account, while the reverse is less frequent. Inferences about what selection pressures must have shaped the social life of our ancestors derived from the social psychology of living humans are generally going to be more secure than inferences about living behavior from an inevitably poorly understood past. The details of how cognition is organized may bear some stamp of its complex historical trajectory. Reductionist psychology gives us the means to reverse engineer a complex design by tearing it to pieces to see how it works. The intricacies of a particular complex design are apparent in such exercises. We certainly should not discount roles for evolutionary theory or for paleoanthropology in understanding human behavior. They have essential tools, so long as these tools' limitations as well as their strengths are understood. Guessing from basic evolved functions about how an organism will fulfill these functions is forward engineering. If the design problem is complex, even great guesses will almost certainly only lead to organisms that might have been. Like economics and meteorology, evolutionary science is only weakly predictive. Nevertheless we take full advantage these sciences' weak predictions because in important domains they are the best we can do. Still, a good understanding of living human minds, a reasonably paleoanthropological record, and a body of well-verified theory may altogether be insufficient to

trace the details of the trajectory a complex adaptation took through a rugged fitness topography.

8. CONCLUSION

Humans are a difficult species. The Darwinian project is committed to bringing us into the same basic explanatory framework as all other organisms. In his M notebook on August 16 1838, while he was in full pursuit of his first formulation of natural selection, Darwin wrote "Origin of man now proved.—Metaphysics must flourish.—He who understand baboon would do more toward metaphysics than Locke" (Barrett, 1974: 281). Darwin realized that failing to account for human behavior left a dangerous gap in his theory through which opponents could and did try to attack his whole theory. When, in the *Descent of Man*, Darwin reluctantly undertook to explain our species, a hostile commentator in the Quarterly Review, whom Darwin believed to be his persistent critic St. George Mivart, took advantage of perceived problems in the human story to attack the whole ediface. The reviewer gloated, it "offers a good opportunity for reviewing his whole position" (and rejecting it, Anonymous, 1971). If the gap between humans and our animal ancestors is too large, it is difficult to explain how ordinary evolutionary processes could explain our origins. If one species escapes the net of evolution by natural selection, the whole of so comprehensive a theory is brought into question. On the other hand, a considerable gap between our ape ancestors and ourselves exists and must be explained, if only to account for our ecological success. Our nearest living ancestors are forest dwelling creatures with modest ranges and abundances. Our more immediate fossil ancestors began to extend their ranges beyond Africa a million or so years ago. Even then, the range of *Homo erectus* and related hominids was not strikingly greater than that of some large carnivores like lions and pumas. However, by latest Pleistocene times, *Homo sapiens*, using toolkits of great sophistication, penetrated to the furthermost reaches of the Old World. With the waning of the ice at the end of the Pleistocene we exploded into the New World. In the Holocene, human societies have rapidly become very complex, rivaling in this regard the eusocial insects. In the industrial era, we are coming to have climatic impacts that rival the drivers of the Pleistocene.

Only in the late 20th Century did evolutionary biologists become markedly more sophisticated than Darwin about the evolution of behavior. W. D. Hamilton's (1964) famous papers on inclusive fitness launched the theoretical study of social evolution, and a growing corps of empirical ethologists began conducting theoretically relevant investigations. Richard

Alexander's (1974) review paper and Edward Wilson's (1975) treatise Sociobiology left no doubt that evolutionary biologists were going to apply this theory to humans with little or no respect for claims of disciplinary autonomy based on superorganic claims for cultural processes. At the same time, the population geneticists Lucca Cavalli-Sforza and Marcus Feldman (1973) initiated the study of cultural evolution using a style of mathematical modeling borrowed from population genetics. Other threads important to the problem of understanding humans in a comparative framework were picked up in that period. For example, Bennett Galef (1977) began his important work on social learning in Norway rats, and the first deep-ocean cores began to reveal the true dimensions of Pleistocene climates. Advances in paleoanthropology in recent years have likewise been spectacular.

Twenty-five years of relatively intensive work have many important questions outstanding. This essay is an attempt to link the results from theoretical modeling the evolutionary properties of culture with some relevant sets of empirical work to produce a synthetic hypothesis to explain the origin of human culture. We make no strong claims for its particular postulates. Our frequent repetition of the word "perhaps" and its relatives emphasizes our belief that many important questions remain to be answered. We believe much more strongly that the main hypothesis here has the right general ingredients to be a successful explanation. It takes a stab at addressing the adaptive economics of large brains and connecting these considerations to the environmental changes that must have driven the encephalization trends of the Cenozoic. It takes a stab at explaining how humans, so lately derived from ancestors with relatively modest systems of social learning, could at once be spectacularly successful using culture but yet not have a crowd of competitors for the cultural niche.

The hypothesis makes predictions that are testable. If it is true, the pattern of climatic deterioration of the Cenozoic should predict the pattern of mammalian encephalization. The correlation is good back 6 million years, and it appears that the step-wise climate deterioration is mirrored in events in hominid evolution (deMenocal & Bloemendal, 1995). It should also hold for the more modest mammalian brain size increases of the middle and early Cenozoic. If selection cannot favor a capacity for complex culture when it is rare, we should expect that apes will show preadaptations for culture. That is, they should have cognitive capacities that are homologous to those that we use to support complex, cumulative culture, but that are subsidized, if not entirely supported by, other functions. Chimps and orangutans have some capacity for imitation that is apparently little if at all used in the wild. What function does it serve? Similarly, if parrots and other animals do prove to have capacities for imitation that might support complex cultural traditions, they should serve other functions. Do humans adaptively vary in their relative reliance on cultural tradition versus

individual learning as the theoretical models suggest that they should? Do the simple systems of social learning that are probably common in social animals serve the function of adaptation to autocorrelated variable environments? The empirical support for the climate deterioration hypothesis comes from climate proxy data that are mostly very far from measuring variations relevant to the fitness of particular organisms. Only the beautifully detailed ice core data permits us to look at variation on the generational time scale. Beyond about 420,000 years ago, the ice core record disappears and we have only the coarser scale of deep-sea cores. Much more will be revealed in the future, for example from cores from deep, old lakes like Lake Tanganyika.

The hypothesis that social learning is a common adaptation to variable environments could be refined if the proximal features of cognition were better understood. The cognitive economy of brains is, despite much recent attention to other aspects of cognition, poorly understood. Is the incremental cost of improving simple social learning at a given level of individual learning really small? Is it true that even relatively rudimentary imitation requires costly cognitive machinery, making it impossible for selection to favor true imitation incrementally, beginning with rather simple traditions and working smoothly towards complexity on the human scale? What are the advantages and disadvantages of coding adaptations to variable environments as innate rules versus using more general rules supplemented by learning or social learning? How do individual learning, and social learning interact to support complex cognitive abilities? The rudimentary considerations introduced here suggest that something much more complex than a simple tradeoff between them.

The simple models about the evolutionary significance of culture, upon which the climate driven hypothesis is based, make only very general predictions about how organisms will respond to a variable environment, but they hold out the hope of robust results. Improving upon such predictions is difficult. This does not mean that we need to despair about ever understanding the origins of the human mind. Success in reconstructing the evolution of human minds will come from triangulating on our mysterious past from many different perspectives. No one technique such as strategic modeling by itself will advance understanding more than marginally. In this chapter, we have tried to show how testing the models' predictions against the large scale patterns of mammalian brain enlargement, and of the environmental changes that presumably drove encephalization, sheds some light on the issue. These data constrain the universe of plausible hypotheses, and will exert tighter constraints as they get better. Other kinds of data constrain them still further.

We must take care not to ask science to solve the insoluble. Meteorologists have had to get comfortable with the idea that chaotic dynamics

put fundamental limits on weather prediction. Brandon (1990) observes that evolutionary accounts are generally "how possibly" rather than "how actually" explanations because of practical if not fundamental limits on what we know and can hope to know about evolutionary trajectories. How possibly explanations do give us some real insights into evolutionary processes. We can at least aspire to better understand whether or not the evolution of human cognition was a complex design process or not. If so, we should get comfortable with the idea that the multi-optimality of complex design problems, combined with the paucity of data about the past, put fundamental limits on our ability to understand how we came to be what we are. Not to mention what we might become. Some research programs—we have singled out innatist evolutionary psychology—defy what seem to us to be fundamental limits on the level of detail that strategic modeling can hope to produce.

Thus, the challenge of the origin of the human mind is much the same as it was in Darwin's day. Humans must have evolved by the same basic processes as other organisms yet we are highly unusual in our mode of adaptation by cultural traditions and in our ecological success. Quite likely, the climatic deterioration of the late Cenozoic, especially of the Pleistocene, played a key role in the evolution of culture. Capacities for social learning expanded as a means of adapting to the highly variable environment of the ice age, probably in many mammalian lineages. However, only our species went on to evolve the capacity to acquire complex cultural traditions by imitative social learning. The events leading up to the late Paleolithic expansion in cultural complexity remain obscure, but some form of preadaptive breakthrough hypothesis is supported by the current evidence.

ACKNOWLEDGMENTS

We thank Nicholas Thompson and Francois Tonneau for their highly constructive criticism of the first draft of this paper. Thanks also the participants in the 5th Biennial Symposium on the Science of Behavior: Behavior, Evolution, and Culture in Guadalajara, Mexico, February 1998, for many thoughtful comments.

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Chapter 2

THE EVOLUTION OF LIFE HISTORY, INTELLIGENCE AND DIET AMONG CHIMPANZEES AND HUMAN FORAGERS

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ABSTRACT

Compared to those of other primates and mammals, human life histories exhibit at least four distinctive characteristics: (a) an exceptionally long lifespan, (b) an extended period of juvenile dependence, (c) support of reproduction by older, post-reproductive males and females, and (d) male support of reproduction through the provisioning of females and their offspring. Another distinctive feature of our species is a large brain size and its associated psychological attributes: increased capacities for learning, cognition and insight. Humans and chimpanzees, compared to other primates, lie closely on a dietary continuum that emphasizes difficult-to-acquire foods. However, the extreme commitment of humans to such a diet has led to distinctive life history traits and age profiles of food production. What underlies these features is a qualitative difference in the role of males through their provisioning of meat to females and young. Meat is a preeminently provisionable resource of great value to growth and reproduction, but its acquisition comes at the cost of both skill and risk. The commitment of human males to specialize in this enterprise is the foundation of the four distinctive characteristics of human life histories. In this

Perspectives in Ethology, Volume 13: Evolution, Culture, and Behavior
edited by Tonneau and Thompson, Kluwer Academic/Plenum Publishers, New York, 2000

chapter, we propose a theory that unites and organizes these observations through comparisons of the behavior, biology, and life histories of chimpanzees and humans.

1. INTRODUCTION

Chimpanzees and humans share approximately 98.5% of their genes (Goodman, 1999). The two species' cognitive capacities and social behavior also express striking commonalty in their high levels of socially-transmitted behaviors, patterns of food procurement that include extractive foraging and the hunting and social exchange of meat, fission/fusion male-bonded social systems, similar patterns of social alliances and conflict resolution, and cognitive behaviors which suggest a concept of the minds of others as well as quantitative representation. The impressive display of commonalties shared by chimpanzees and human foragers in numerous aspects of their biology and behavior pushes us to consider whether many of the differences between the two species are a matter of degree or, if we explore the major parameters of their life course and feeding niche, we will find distinctions which set the two species apart. In other words, what are the major distinctions between human foragers and apes in their adaptive niches? And, can we best understand the distinctively human life history traits as co-evolved features associated with human entrance into a unique feeding niche?

Our theory is that those four life history characteristics as well as extreme intelligence are co-evolved responses to a dietary shift towards high-quality, nutrient-dense, and difficult-to-acquire food resources. The underlying logic is the following. First, high levels of knowledge, skill, coordination and strength are required to exploit the suite of high-quality, difficult-to-acquire resources that humans consume. The attainment of those abilities thus requires time and a significant commitment to development. This extended learning phase, during which productivity is low, is compensated by higher productivity during the adult period, with an intergenerational flow of food from old to young. Since productivity increases with age, the time investment in skill acquisition and knowledge leads to selection for lowered mortality rates and greater longevity, because the returns on the investments in development occur at older ages. This in turn will favor a longer juvenile period if there are important gains in productive ability with body size, and growth ceases at sexual maturity. Second, we believe that the characteristics of the feeding niche, with associated food sharing, provisioning of juveniles, and increased grouping led to lower mortality during the juvenile and adult periods, because provisioning assists

recovery in times of illness or injury and reduces risk by limiting juvenile time allocation to foraging. These buffers against mortality also favor a longer juvenile period and higher investment in other mechanisms to increase life span.

Thus, we propose that the long human life span co-evolved with the lengthening of the juvenile period, increased brain capacities for information processing and storage, and intergenerational resource flows—all as a result of an important dietary shift. Humans are specialists in that they only consume the highest quality plant and animal resources in their local ecology and rely on creative, skill-intensive techniques to exploit them. Yet, the capacity to develop new techniques for extractive foraging and hunting allows them to exploit a wide variety of different foods and to colonize all of the Earth's terrestrial and coastal ecosystems.

2. CHIMPANZEE CULTURE AND HOMINID EVOLUTION

The recognition and identification of socially transmitted, locally variable, adaptive behavior patterns among chimpanzees have been the focus of numerous recent books and publications (Byrne, 1995; Heltne & Marquart, 1989; McGrew, Marchant, & Nishida, 1996; Whiten et al., 1999; Wrangham et al., 1994). It is clear that chimpanzees use socially transmitted behavioral patterns to solve many of the most critical challenges posed by natural selection, such as finding food, acquiring mates, forming social alliances, and raising young. These behavioral patterns vary from one study location to another and arguably can be identified as local social traditions. In a comprehensive review of chimpanzee cultures, Whiten and associates (1999), using 151 years of chimpanzee observations from seven long-term studies, found 39 behavior patterns that were customary or habitual in some communities but were absent in others and could not be explained by ecological differences. Furthermore, studies of captive chimpanzees indicate that chimpanzee cognition and intelligence may combine features of learning processes, self-awareness, and ability to communicate that are critical underpinnings to human culture. Finally, some essential features of chimpanzee and human social behavior are shared, indicating that certain features of chimpanzee social organization that strongly affect life history strategies are similar to those of humans.

Food-procurement patterns of chimpanzees are notable for two critical features which link them to human behavior: The inclusion of extractive foraging techniques and the hunting of meat (Gibson, 1986; Parker & Gibson, 1979; Stanford, 1998, 1999). The behavior patterns involved indicate slow acquisition of skills during development (Boesch & Boesch, 1999;

Goodall, 1986) as well as variability from one study site to the next (Whiten et al., 1999). Chimpanzee use of tools as aids to extractive foraging has been well documented (Boesch-Achermann & Boesch, 1994; Byrne, 1997; Sugiyama, 1997). Tool use has been described at all the major study sites for chimpanzees and includes a long list of sponging, fishing, digging, and cracking behaviors, all of which give chimpanzees access to drinking and food resources which are much less efficiently extracted by bare hand or perhaps not at all. Furthermore, in some sites such as the Tai Forest, stone bashers and anvils are regularly used. Of the 39 behaviors that Whiten and associates felt confident enough to label cultural traditions, 19 were patterns of extractive foraging (an additional 14 extractive foraging behaviors were identified but failed to achieve these researchers' criteria of habitual status in any one community). Although the calories gained from both extractive foraging and hunting are a relatively small percentage of the total diet as measured both by time spent feeding and by caloric value, this aspect of chimpanzee behavior indicates a species' interest in hard-to-acquire, nutritionally dense foods which is expressed in ecologically diverse habitats (Goodall, 1986; Tutin et al., 1992; Whiten et al., 1999).

Another feature of chimpanzee behavior that has attracted the attention of evolutionary socioecologists is a pattern of group formation which is unusual by nonhuman primate standards. Chimpanzee social organization is characterized by male philopatry, female migration at puberty, bonding between male relatives, and the collaboration of bonded males in the defense of resident females against other male-bonded groups and sometimes in hunting as well (Nishida & Hosaka, 1996; Stanford, 1998; Wrangham & Peterson, 1996). This complex of organization patterns is clearly shared with humans, another species characterized by male bonding and collaboration for aggression and defense.

The alliances formed by chimpanzees for the purposes of gaining and defending mates, social status, and feeding territories, are supported by a repertoire of behaviors also shared by humans. De Waal (1996) and Hemelrijk (1996) describe social alliances and conflict resolution through reciprocity, reconciliation and a form of negotiation through conflictive interactions. Even more interestingly, Goodall (1986), Tutin (1979), and Stanford (1998, 1999) all describe the use of hunted meat as a medium of social exchange for access to both sex and power by chimpanzee adult males. Similar use of meat as a social token by human foragers has been proposed by Hawkes (1991) and investigated by Kaplan and Hill (1985a, 1985b). Food sharing in general is such a critical feature of the human adaptive pattern (in which adults feed young, and males and females share collected and hunted foods) that any food sharing in chimpanzees arouses great interest in the scientific community (Rose, 1997; Winterhalder, 1996).

So far, food sharing is reported to be by chimpanzee mothers to offspring, for hard-to-process foods (Boesch & Boesch, 1999; Hiraiwa-Hasegawa, 1990b; Silk, 1978, 1979), by males to female sexual partners, for meat (Stanford, 1998; Tutin, 1979), and by possessors of meat to social allies and close kin (Boesch & Boesch, 1999; Stanford, 1998; Tutin, 1979), all of which are identified as typically human sharing behaviors.

The question of chimpanzee intelligence, their cognitive abilities, the mode of transmission from one generation to the next of locally variable, adaptive behavior patterns, and the extent to which chimpanzees are able to interpret the behaviors and understand the thinking processes of other chimpanzees can only be fully investigated in captivity (Boysen, 1994; deWaal, 1992; Matsuzawa, 1996; Povinelli, 1994; Tomasello, 1994). Byrne (1995) has argued cogently that great apes and humans are set apart from other primates in their ability to acquire novel behavior patterns though imitation—a quick way of acquiring a complex skill while avoiding time-consuming and potentially dangerous errors. The ability to imitate would be especially significant to a species which depends on skills-based performances for extractive foraging and hunting. Although the notion of a cognitive split between humans and apes and other primates may be defended, the intelligence of chimpanzee behavior in the laboratory suggests a theory of the mind (de Waal, 1992; Povinelli, 1994; Tomasello, 1994), some ability to manipulate numbers (Boysen, 1997), and the use and manipulation of symbols (Rumbaugh, Savage-Rumbaugh, & Sevcik, 1994).

In summary, research on chimpanzee behavior in both the wild and captivity in the past ten years provides ample evidence of communalities between humans and chimpanzees in extractive foraging and hunting, social learning and intergenerational transmission of complex behaviors, social organization, behavioral patterns of social affiliation and conflict, and intelligence and cognition. The question remains as to whether these considerable communalities in behavior between humans and chimpanzees have had the same impact on the life histories of both species and on the configuration of the feeding niches they occupy.

3. LIFE HISTORIES OF HUMAN FORAGERS AND WILD CHIMPANZEES

Although both chimpanzees and humans are large-bodied, long-lived mammals, their life histories differ in various critical parameters: survivorship to age of first reproduction, life expectancy at the beginning of the

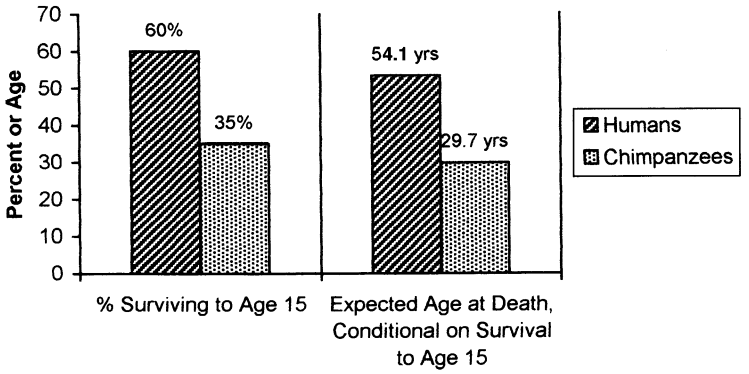

Figure 1. Survival to age 15 and adult lifespan: Human foragers and chimpanzees.

reproductive period, absolute and relative length of the post-reproductive period, spacing between births of surviving offspring, and growth during the juvenile period (Hill & Kaplan, 1999; Kaplan, 1997). The differences between traditional human forager and chimpanzee life spans are shown in Figure 1, and life history traits for the two species are compared below in Table 1.

Table 1 summarizes human life history parameters based on data from four extant groups of human foragers: Ache (Paraguay), Hadza (Tanzania), Hiwi (Venezuela), and !Kung (Botswana/Namibia); see Kaplan, Hill, Lancaster, and Hurtado (1999, table footnotes) for detailed accounts of the sources of the data and how each value was calculated. The forager data come from studies on populations during periods when they were almost completely dependent on wild foods, with little modern technology (and no firearms), no significant outside interference in interpersonal violence or fertility rates, and no significant access to modern medicine. Table 1 also presents chimpanzee life history parameters based on data from five extant groups of chimpanzees: Bossou (Guinea), Gombe (Tanzania), Kibale (Uganda), Mahale (Tanzania) and Tai (Ivory Coast). The chimpanzee data have been compiled from all published and unpublished sources that we are aware of, and, because of small sample size at individual sites, mortality data were combined to create a synthetic life table encompassing all data for wild chimpanzees (Hill et al., 1999).

The data suggest that forager children experience higher survival to age 15 (60% vs. 35%) and higher growth rates during the first five years of life (2.6 kg/yr. vs. 1.6 kg/yr.) than do chimpanzee juveniles. Chimpanzees, however, grow faster between ages 5–10 both in absolute [2.5 kg/yr. (chimpanzees) vs. 2.1 kg/yr. (humans)] and proportional weight gain (16% per

Table 1. Life history parameters of human foragers and chimpanzees (after Kaplan, Hill, Lancaster, & Hurtado, 1999).

Group	Probability of survival to age 15	Expected age of death at 15 (years)	Mean age first reproduction (years)	Mean age last reproduction (years)	Inter-birth Interval* (months)	Mean weight age 5 (kgs.)	Mean weight age 10 (kgs.)
Humans							
Ache female	0.61	58.3	19.5	42.1	37.6	15.7	25.9
Ache male	0.71	51.8				15.5	27
Hadza female	0.58	54.7				15.5	20
Hadza male	0.55	52.4				14.2	21.2
Hiwi female	0.58	51.3	20.5	37.8	45.1	18	29.8
Hiwi male	0.58	51.3				16.4	33.6
!Kung female	0.6	56.5	19.2	37	41.3	14	19.5
!Kung male	0.56	56.5				16	22.5
Forager mean	**0.60**	**54.1**	**19.7**	**39.0**	**41.3**	**15.7**	**24.9**
Chimpanzees							
Bossou female					51		
Bossou male							
Gombe female	0.545	32.7	14.1		64.6	10	21
Gombe male	0.439	28.6				10	24
Kibale female	0.805	35.6			68		
Kibale male	0.408	40.6					
Mahale female			14.6		72		
Mahale male							
Tai female	0.193	23.8	14.3		69.1		
Tai male	0.094	24					
Chimpanzee mean	**0.35**	**29.7**	**14.3**	**27.7****	**66.7**	**10**	**22.5**

* Mean inter-birth interval following a surviving infant.
** Age of last reproduction for chimpanzee females was estimated as two years prior to the mean adult life expectancy.

year vs. 10% per year (see Table 1). The earlier high weight gain in humans may be due to an earlier weaning age (about 2.5 years vs. about 5 years for human foragers and chimpanzees respectively) and by parental provisioning of highly processed foods. The later slow growth of human children between 5–10 years is intriguing. According to the allometric growth law, mammalian growth is described by the equation $dw/dt = Aw^{0.75}$. Most mammals show a yearly growth constant, A, of about 1 whereas the mean primate value for A is about 0.4 (Charnov, 1993). Forager children between ages 5–10 are characterized by a growth constant around 0.2.

The chimpanzee juvenile period is shorter than that for humans, with chimpanzee females giving birth for the first time about five years earlier than hunter-gatherer women. This juvenile period is followed by a dramatically shorter adult lifespan for chimpanzees. In the wild, surviving 15-year old chimpanzees have a life expectancy of only age 30, whereas hunter-gatherers can expect to live an average of 39.2 additional years, provided they have survived to age 15. Importantly, women spend more than a third of their adult life in a post-reproductive phase, whereas few chimpanzee females spend any time at all in a post-reproductive phase. The differences in terms of overall survival and lifespan are striking when comparing survival probabilities for the two species (Figure 1). Less than 10% of chimpanzees ever born survive to age 40, but more than 15% of hunter-gatherers ever born survive to age 70!

Finally, despite the fact that the human juvenile and adult periods are longer, and that human infants are larger than chimpanzee infants at birth (about 3 kg vs. 2 kg), hunter-gatherer women are characterized by higher fertility than chimpanzee females (Figure 2). The mean inter-birth interval (IBI) between offspring (when the first survives to the birth of the second) is over 1.5 times longer among wild chimpanzees than among modern forager populations. Table 1 indicates that forager women may have somewhat longer reproductive spans on average than chimpanzee females, since over 80% of women in foraging societies survive to the age of last birth, whereas chimpanzee last birth is expected to be about 2.5 years (half an inter-birth interval) before the end of the average lifespan. These numbers lead to an interesting paradox. Life tables from modern human foragers always imply positive growth (discussed in Hill & Hurtado, 1996, Ch. 14), whereas the chimpanzee numbers presented here imply slightly negative population growth rates.

To summarize, human foragers show a juvenile period 1.4 times longer than chimpanzees and a mean adult lifespan 2.5 times longer than chimpanzees. Human foragers show higher survival at all post-weaning ages, but lower growth rates during mid-childhood. Despite a longer juvenile period, a slower growth, and a long post-reproductive lifespan, forager women achieve higher fertility rates than chimpanzee females.

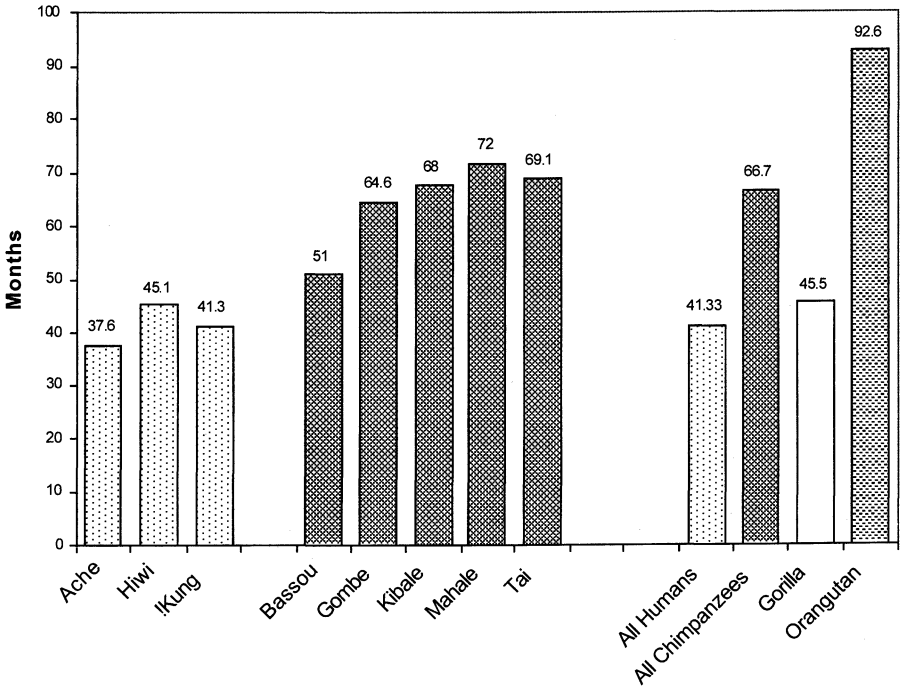

Figure 2. Birth spacing of human foragers and great apes (after Kaplan, Hill, Lancaster, & Hurtado, 1999).

4. CONSUMPTION AND PRODUCTIVITY THROUGH THE LIFE COURSE: CHIMPANZEES AND HUMAN FORAGERS

4.1. Components of the Diet

A comparison of the diets from ten foraging societies and several chimpanzee communities (for which caloric production or time spend feeding were monitored systematically) is summarized in Table 2. Human and nonhuman primate diets can be subdivided into vertebrate animals; roots, nuts, seeds, and other plant parts (leaves, flowers, pith, etc.); and invertebrate animals. Modern human foragers all differ considerably in diet from chimpanzees (see Table 3). Measured in calories, the major component of human forager diets is vertebrate meat, with an approximate range of 20% to 80% of the diet in the sampled societies. Most diets consist in more than 50% of vertebrate meat (equally weighted mean = 60%); the emphasis on vertebrate meat would be even more clear if any Arctic foraging societies

Table 2. Diet of human foragers and chimpanzees (after Kaplan, Hill, Lancaster, & Hurtado, 1999).

	Hunter-Gatherers										Chimpanzees				
	Onge	Anbarra	Arnhem	Ache	Nukak	Hiwi	!Kung[1]	!Kung[2]	Gwi	Hadza		Gombe	Kibale	Mahale	Tai
Sample*	**1,256**	**3,654**	**276**	**3,645**	**941**	**4,756**	**866**	**928**	**?**	**?**	**Sample***				
kg/person day**											**kg/person day****				
meat	0.59	0.58	1.34	1.36	0.62	0.97	0.26	0.59	0.30	1.10	meat	0.03		0.01	0.04
roots	0.21	0.07	0.43	0.00	0.00	0.44	0.15	.	0.40?	1.62	roots				
seeds, nuts	0.00	0.00	0.00	0.00	0.00	0.00	0.21		0.00	0.00	seeds, nuts				
fruits	0.00	0.15	0.01	0.61	0.86	0.29	0.15	.	0.40?	0.54	fruits				
other plant	0.00	0.00	0.00	0.96	0.00	0.04	0.00		0.00	0.00	other plants				
invertebrate	0.01	1.01	0.09	0.11	0.35	0.02	0.00	.	0.00	0.24	invertebrate				
calories/person day***															
meat	980	822	1,821	2,126	764	1,350	690	1,602	417	1,940					
roots	242	93	456	0	0	268	150	.	600?	1,214					
seeds, nuts	0	0	0	0	0	0	1,365		0	0					
fruits	0	44	10	22	747	82	150	.	600?	621					
other plant	0	0	3	255	0	36	0	.	0	0					
invertebrate	20	127	67	308	375	57	0		0	255					
Total	**1,243**	**1,085**	**2,357**	**2,712**	**1,886**	**1,793**	**2,355**	**.**	**1,617?**	**4,030**					
Non foraged[#]	0	1,116	0	trace	378	626	trace	trace	0	trace					
Dietary percentage of foraged foods											**Feeding time percentage**				
meat	**79**	**75**	**77**	**78**	**41**	**75**	**29**	**68?**	**26?**	**48**	**meat**	**1.5**	**0.9**	**2.5**	**2.1**
roots	**19**	**8**	**19**	**0**	**0**	**15**	**6**	**.**	**37?**	**30**	**roots**	**0.0**	**0.1**	**0**	**1.4**
seeds, nuts	**0**	**0**	**0**	**0**	**0**	**0**	**58**		**0**	**0**	**seeds, nuts**	**5.1**	**0**	**0**	**7**
fruits	**0**	**4**	**0**	**1**	**40**	**5**	**6**	**.**	**37?**	**15**	**fruits**	**60.2**	**78.5**	**57.7**	**67.6**
other plant	**0**	**0**	**0**	**9**	**0**	**2**	**0**		**0**	**0**	**other plant**	**29.3**	**21.3**	**33.4**	**15.5**
invertebrate	**2**	**12**	**3**	**11**	**20**	**3**	**0**	**.**	**0**	**6**	**invertebrate**	**3.9**	**0**	**6.4**	**5.6**
collected	**0.0**	**4.0**	**0.6**	**0.8**	**20?**	**4.6**	**4.9**	**?**	**37?**	**15**	**collected**	**94.2**	**99.1**	**91.1**	**92.3**
extracted	**21.9**	**20.3**	**30.1**	**24.3**	**40?**	**21.6**	**63.4**	**?**	**37?**	**36**	**extracted**	**3.8**	**0**	**6.4**	**5.6**
hunted	**78.0**	**75.7**	**69.4**	**74.9**	**40**	**73.7**	**31.7**	**68.0**	**26.0**	**48**	**hunted**	**2**	**0.9**	**2.5**	**2.1**

* Person days sampled including all men women and children as equal consumers.
** This is the weight of the edible portion for meat and field weight for all other resources.
# Intake of non-foraged foods in calories/person day when measured or reported.

Table 3. Production of energy by men and women in 10 foraging societies (after Kaplan, Hill, Lancaster, & Hurtado, 1999).

		Mean daily adult production (calories)	% total adult calories	% total adult protein
Onge	men	4,000	79.7	94.8
	women	1,021	20.3	5.2
Anbarra	men	2,742	70.0	71.8
	women	1,174	30.0	28.1
Arnheim	men	4,578	69.5	93.0
	women	2,012	30.5	7.0
Ache	men	5,590	84.1	97.1
	women	1,055	15.9	2.9
Nukak	men	4,556	60.4	98.6
	women	2,988	39.6	1.4
Hiwi	men	3,489	79.2	93.4
	women	916	20.8	6.6
!Kung[1]	men	3,221	45.5	44.7
	women	3,864	54.5	55.3
!Kung[2]	men	6,409	>>50	
	women			
Gwi	men	2,412	43.0	78.7
	women	3,200	57.0	21.3
Hadza	men	8,089	64.8	100
	women	4,397	35.2	0

were included in the sample. In contrast, chimpanzees spend about 2% of their feeding time eating meat. Unfortunately, the diet of wild primates is not usually expressed in calories as is the human forager's. Field workers usually estimate the food energy acquired from the time spent feeding on various food types, and rarely express their data in terms of calories consumed. The absolute intake of meat per day also varies tremendously, the chimpanzee per capita meat intake being estimated at about 10–40 grams per day, whereas human diets range from 270 to about 1,400 grams per person per day. Even though chimpanzee males eat much more meat than do females and juveniles (Boesch & Boesch, 1999; Stanford, 1998, 1999; Wrangham, Van, & Riss, 1990), in general members of foraging societies eat more than ten times as much meat as do chimpanzees.

The next most important food category in our forager sample is roots (an extracted resource), which make up an average of about 15% of the energy in the forager diet, and are important in about half the societies in our sample (Table 2). In contrast, the chimpanzee diet is primarily (over 90%) comprised of collected (as opposed to extracted or hunted) foods. However, within the category of collected foods (which includes leaves,

flowers, pith, unripe and ripe fruit), chimpanzees concentrate on the resource of the highest quality and most difficult to acquire, ripe fruit, over 60% of their feeding time being spent on that resource type alone. Only two foraging societies eat large amounts of ripe fruit: the Gwi San of the Kalahari Desert, who consume melons for water and some nutrients during much of the year, and the Nukak of Colombia who extensively exploit tropical palm fruits. Likewise, other, less nutritive plant products are an important secondary food for chimpanzees, making up about 25% of observed feeding time. This category is unimportant for the foragers in our sample, with the exception of the Ache who regularly extract starch and growing shoots from tropical palms.

Figure 3 summarizes the comparison of the diets of human and nonhuman primates presented in Table 2. Extensive overlap between the human foragers' and chimpanzee diets is obvious, yet the data indicate that humans specialize in rare but nutrient-rich resource patches (meat, roots, nuts) whereas chimpanzees specialize in ripe fruit and plant parts with a low density of nutrients. The human diet especially features foods coming in packages that are not only nutritionally dense, but also require skills to obtain. Chimpanzees, on the other hand, depend mostly on collected, ripe fruits with small supplements of insects, extracted foods and small game. Big game (larger than the body size of the individual hunter) is a human prerogative. These fundamental differences in diet are reflected in the gut morphology and food passage times of chimpanzees and humans (Milton, 1999). Chimpanzees are more committed to the rapid passage of bulky, fibrous meals processed in the large intestine whereas humans process

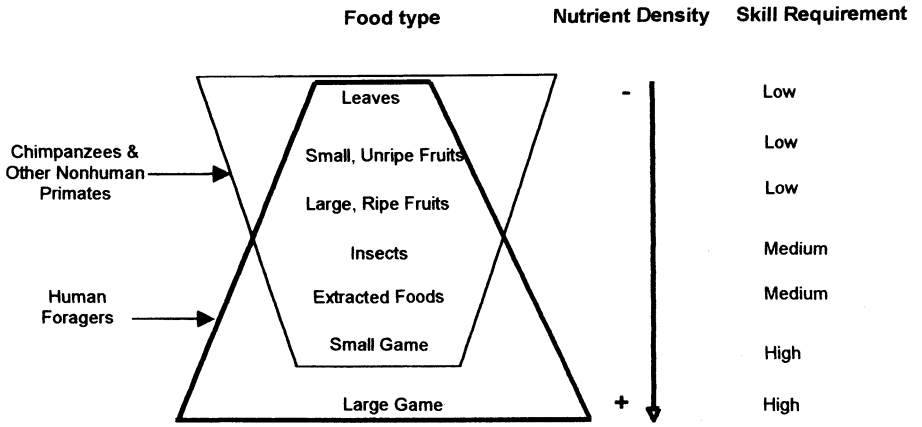

Figure 3. Feeding ecology of human foragers and other primates (after Kaplan, 1997).

nutritionally dense, lower volume meals amenable to slower digestion in the small intestine.

4.2. Difficulty of Acquisition

The key feature of our theory linking feeding niche to life history concerns the relationships between difficulty of acquisition and the age patterning of production for humans and chimpanzees. In order to compare difficulty of acquisition across ecologies, it is useful to rank resources into three different classes going from most easily to most difficult to acquire. *Collected resources* are the easiest to acquire; they are sessile, plant resources which can be gathered and consumed without significant processing. Examples of collected resources are most fruits, leaves, flowers, and sprouts. *Extracted resources* are more difficult to acquire, because their consumption involves extraction of the food contents (most often the reproductive or energy storage organs of plants or animals) from a protective environment such as hard shells or the underground, or because the food is saturated with toxins which may demand extensive processing. Examples of extracted resources are roots and tubers, nuts, insects in protected nests, honey, palm fiber, and some seeds. Lastly, *hunted resources* are the most difficult to acquire, because they are mobile and engage in either evasion or active defense. Hunted resources in relatively large packages are especially dangerous to hunt even if prey body size is less than that of an individual hunter. Clearly, this categorical scheme is rough, because it does not take into account variation within categories or dependence on technology. However, the three categories do capture the major differences between human and chimpanzee strategies for food acquisition.

A breakdown of forager and chimpanzee foods by our three acquisition categories show that chimpanzees obtain an average of about 95% of their diet from collected foods, whereas the foragers in our sample obtain an average of 8% of their food energy from collected resources (Kaplan et al., 1999). On the other hand, foragers obtain about 60% of their food energy from hunted resources and about 32% from extracted resources, whereas chimpanzees obtain about 2% of their food energy from hunted foods and about 3% from extracted resources. Even though the categories may be somewhat rough, humans are clearly much more dependent than chimpanzees on food resources that require complicated techniques to obtain. It is also the case that there is a wide variability in human diet based on the availability of nutrients in the local environment. In all environments, however, humans tend to eat the best, most concentrated food using their skills in extraction and hunting.

4.3. The Age and Sex Patterning of Food Acquisition and Consumption among Chimpanzees and Humans

Data on food acquisition by age and sex category only exist for three modern foraging populations. Ache and Hiwi food production was monitored directly throughout most months of various years by weighing all food produced by foragers of different age and sex categories (Hill et al., 1984; Hurtado & Hill, 1990). Hadza women's and children's plant food acquisition was estimated indirectly from samples of in-patch return rates for different fruit and root resources, over various age/sex classes, during part of the wet and part of the dry season of various years (Hawkes et al., 1989, 1995; Blurton Jones et al., 1989, 1997). These data were combined with sample estimates of time spent foraging and frequency of foraging across days to estimate daily food acquisition (e.g., Blurton Jones et al., 1989, 1997). Men's food acquisition from hunting was measured directly by weighing all large game brought to the camp (Hawkes et al., 1992).

All three societies show a similar pattern, presented separately for males and females in Figures 4 and 5. Forager children produce little food compared to adults. In the late juvenile period, daily food acquisition rates

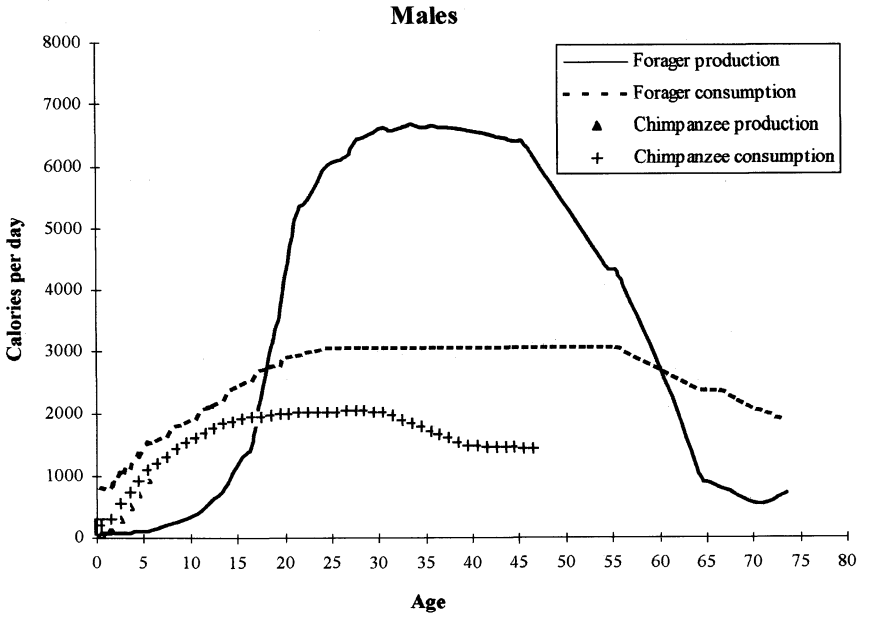

Figure 4. Production and consumption of food: Male foragers and chimpanzees (after Kaplan, Hill, Lancaster, & Hurtado, 1999).

rise dramatically (especially for males) and keep increasing until mid-adulthood (males) or even later (some females). Adult men acquire much more food than any other age/sex category. Although the patterns for men seem consistent for all three societies, Hadza children and post-reproductive women appear to acquire substantially more food than their Ache and Hiwi counterparts (Hawkes et al., 1992, 1997, 1998).

The food consumption rates of forager children and adults can be estimated from body weight and total group production (see Kaplan, 1994). Chimpanzee energy acquisition, while not measured directly, can be estimated from body size and caloric requirements since very little food is transferred between age-sex categories after weaning. This means simply that daily food acquisition and consumption rates are virtually the same for chimpanzees from the juvenile period onward. Figures 4 and 5 show the mean daily energy consumption and acquisition rates for all three hunter-gatherer societies, compared to chimpanzees of the same age and sex.

The human consumption-acquisition profile is strikingly different from that of chimpanzees, with young chimpanzees acquiring considerably more energy than forager children until about the age of sexual maturity. In particular, consumption is greater than acquisition for female

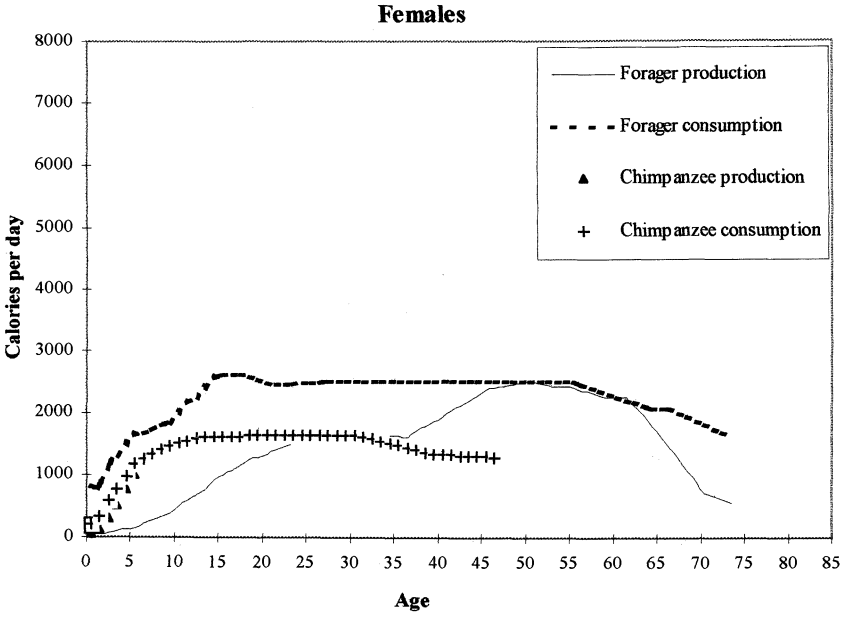

Figure 5. Production and consumption of food: Female foragers and chimpanzees (after Kaplan, Hill, Lancaster, & Hurtado, 1999).

chimpanzees under 10. This reflects several facts of life of chimpanzees. First, they have a long lactation period (nearly 5 years) during which the infant gradually learns to feed itself. Once weaned, nutritional deficits are small and are covered by maternal food sharing of hard-to-acquire foods (Hiraiwa-Hasegawa, 1990a, 1990b; Silk, 1978). By the age of 10 (early adolescence), the chimpanzee youngster is entirely self-feeding, and for the rest of her life produces what she consumes with little surplus. Female chimpanzees do not have more than one nutritionally dependent offspring at a time, and offspring births are widely spaced (5–1/2 yrs.). In contrast, before their late teens children in any forager society produce less than young chimpanzees do. Thus, human juveniles, unlike chimpanzee juveniles, have an evolutionary history of dependency on adults to provide their daily energy needs. Notice that by age 15, the children in our forager sample have reached over 25% of their lifetime energy consumption, but less than 5% of their lifetime energy acquisition.

The areas in Figures 4 and 5 where food acquisition is greater than consumption (where for each species the solid line is above the dotted line) represent surplus energy provided during the later part of the lifespan. The averaged data imply that hunter-gatherer men provide most of the energy surplus that is used to subsidize juveniles and women of reproductive age. While based on only three societies, this average trend can be confirmed by comparing food acquisition rates of adult males and females in the ten forager societies in which food acquisition has been measured within a systematic sample (Table 2).

Food acquisition levels indicate that forager women take much longer to reach peak productivity than men do. Forager males begin to acquire more energy than they consume in their late teens; however, their peak productivity builds slowly from the early twenties to the early thirties and is then sustained for 20 or more years at a level of approximately 6,500 k/cals. per day. In contrast, forager women consume more than they produce until menopause, at which time their consumption matches production for perhaps 20 additional years (although, as mentioned above, there is variability among forager groups).

The causes for this disparity between the age when production and consumption are matched and the absolute levels of peak production are quite different for the two sexes. Male energy acquisition depends largely on the hunting of meat. In order to understand why hunting requires so much learning and practice, a detailed analysis of the skills involved in successful hunting must be carried out. Although a thorough treatment of the topic is beyond the scope of this chapter, a few illustrative comments will prove useful. Not all hunting niches necessarily require intensive learning and cognitive machinery. Sit-and-wait ambush predators, or those who simply move until they encounter vulnerable prey and then chase them

down, may not show great increases in success rate dependent on learning. However, the human hunters that we and others (Lee, 1979; Liebenberg, 1990) have observed use a multitude of information to make contingency-specific decisions both during the search phase of hunting and after encountering prey. Specifically, information on ecology, seasonality, current weather, expected animal behavior, and fresh animal signs are all integrated to form multivariate mental models of encounter probabilities which guide the search and are continually updated as conditions change. Various alternative courses of action are constantly compared and referenced to spatial and temporal mental maps of resource availability. This information is collected, memorized and processed over much larger spatial areas than chimpanzees ever cover. For example, interviews with Ache men show that fully adult men (aged 35+) had hunted in an area of nearly 12,000 km^2 of tropical forest in their lifetimes (Hill & Hurtado, 1996). Almost all foragers surveyed used more than 200 km^2 in a single year, and many covered more than 1,000 km^2 in a year (Kelly, 1995, Table 4.1). Male chimpanzees, on the other hand, cover only about 10.3 km^2 in a lifetime (Wrangham, 1975; Wrangham & Smuts, 1980).

After potential prey are encountered, humans also employ a wide variety of techniques to obtain them, with an astounding creativity. Here are just some examples that Hill, Hurtado and Kaplan have seen among the Ache and Hiwi: Arboreal animals are shot with arrows from the ground or in a tree, driven by climbing, shaken down from branches, frightened into jumping to the ground, brought down by felling the tree with an axe, lured by imitating calls, lured by making captured infants emit distress calls, captured by spreading sticky resin on branches to trap them, and captured by constructing scaffolding from tree branches and vines. Ground dwelling prey are shot with arrows, driven to other hunters or capture devices, run down upon encounter, slammed to death against the ground, strangled around the neck, or suffocated by stepping on them while trapping them in a tight spot. Burrowing prey are dug out, chopped out of tree trunks, stabbed through the ground with spears, frightened to the point where they bolt from the burrow, smoked out, and captured by introducing a lasso through a small hole. Aquatic prey are shot on the surface, driven into traps, poisoned, shot below the surface, discovered on muddy bottoms by systematically poking the bottom of a pond, and speared underwater by random thrusts in drying lakes. The wide variety of killing techniques motivates humans to search for an equally wide variety of prey. Although all groups probably specialize on the most abundant and vulnerable prey in their area, the total array of species taken is impressive, and probably much larger than that covered by most, if not all, other vertebrate predators. For example, from 1980 to 1996 their sample of weighed prey among the Ache included a minimum of 78 different mammal species, at least 21 species of

reptiles and amphibians, probably over 150 species of birds (more than they have been able to identify) and over 14 species of fish.

Chimpanzees, too, show a somewhat delayed pattern in the development of their extractive and hunting skills (Silk, 1979). Boesch and Boesch (1999) report that, although the easier forms of extractive foraging begin at age 5, skill at nut-cracking does not mature until age 10; the hunting of meat only begins at age 20 and its effectiveness continues to increase for nearly a decade. In contrast to chimpanzees and human men, women foragers show a pronounced delay in the match between food acquisition and consumption, not because they take so long to acquire the needed skills, but because of the classic trade-off faced by women between child-care and provisioning (Hurtado et al., 1992). Many human female foragers consume more than they produce through infancy, childhood, adolescence, and during their reproductive careers. During this time they are nearly continuously lactating and may have older juvenile dependents as well. In other words, unlike chimpanzee females, human females can afford to consume more than they produce and have multiple dependent young as well during reproduction. It may not be until reproduction is completed that they begin to match consumption and caloric acquisition. In some circumstances reproductive females can be highly productive, collecting protein in reef environments (Bird, 1999) or extracting high-energy roots from the ground (Hawkes, O'Connell, & Blurton Jones, 1997). The important point is that women can expect help during their reproductive careers, and that this help often comes in the form of animal protein which requires skill and risk to obtain.

4.4. The Effect of Men's Surplus Energy Production on the Reproductive Lives of Women

Figure 6 compares the acquisition of calories and reproductive status of baboons (Altmann, 1980) with Ache foragers (Hill & Hurtado, 1996). Time spent foraging during the day is presented in relation to reproductive status for female baboons, foraging including both travel time and feeding time. What we see is that mother baboons are hard pressed to meet the demands of lactation. When they must produce energy beyond their own maintenance needs, their daily time budget is stretched to the limit. They cannot afford to increase their travel time, which would be energetically costly especially since they must carry their infants. Instead they increase their feeding time, by reducing resting and socializing to about 15% of the day. Mother baboons thus work harder. In fact female baboons have higher mortality rates when lactating than when cycling or being pregnant (Altmann, 1980).

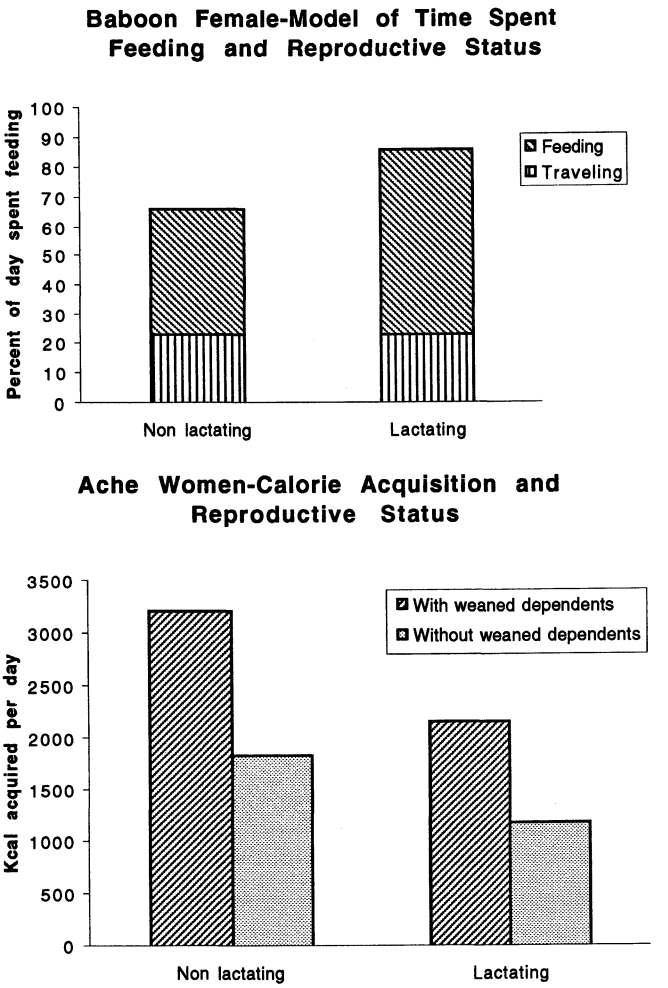

Figure 6. Food acquisition and reproductive status: Ache women and baboon females (Hurtado, Hawkes, Hill, & Kaplan, 1985; Altmann, 1980, p. 56).

Unfortunately, the appropriate data are not available for female chimpanzee productivity, mortality and reproductive status. However, their life history parameters, which include an even longer lactation period with only a single, nutritionally-dependent offspring at a time and no provisioning by other group members, suggest that they too are pressed by the same nutritional stresses as are female baboons.

In contrast, when lactating and even when they have dependent juveniles to be fed, Ache women reduce their work effort (acquisition of food

resources), although not as much as when they have only one nursing infant. Female baboons (and mother chimpanzees as well), on the other hand, never have weaned offspring that are nutritionally dependent. Once they are weaned, young nonhuman primates feed themselves for the rest of their lives whereas just the opposite is true for human juveniles. Human females, then, are able to cut back on energy production when they are nursing even though their caloric consumption and dependency ratio may have gone up, whereas nonhuman primate females increase their work effort during lactation to meet the extra caloric demands of lactation and do not assume juvenile nutritional dependency.

The provisioning of reproductive women and weaned juveniles has a powerful effect on the production of children by humans, and in more than one way: First, it reduces the energy cost and health risk of lactation to the individual mother. Remember Table 1, which shows that most forager women can expect to live out their entire reproductive careers, and that pregnancy and lactation do not raise mortality rates. Second, food provisioning lifts the burden of self-feeding from the shoulders of juveniles, and allows them to remain dependent on adults for energy until they are fully grown. Third, provisioning allows the reduction in birth spacing shown in Figure 2 (Furuichi et al., 1998; Galdikas & Wood, 1990; Kaplan et al., 1999). Since human weanlings do not have to be self-feeders but are provisioned by adults, they can be weaned at an earlier age. The average Inter-birth interval between successive live births of human foragers is around 41 months, which means (allowing 12 months for conception and pregnancy) that most weaning among human foragers occurs about two years and a half after birth.

In contrast, the average inter-birth interval for chimpanzees is 66.7 months, and for orangutans 92.6 months. The only great ape to approach humans in this respect is the gorilla, but the gorilla is an ape that feeds at a very low level of the food chain. The major part of its diet is made of herbaceous plants which are ubiquitous and take little acquired skills to harvest. The main requirement for weaning is that the young gorilla has developed enough gut size to process low-energy foods. On the other hand, women cut back on their work effort and do not produce surpluses during their reproductive careers because their reproduction is being underwritten by other group members, especially men, and not because their productive skills take so long to acquire.

5. CONCLUSIONS

The impressive array of biological and behavioral commonalties shared by chimpanzees and humans might be taken to imply that the

differences between the two species are simply ones of degree. Although some of the features discussed here involve merely quantitative differences, however, others point to distinctions of a qualitative nature. The life history and feeding niche of humans have co-evolved into a unique adaptation which formatted a completely different life course—one characterized by a long period of juvenile dependency, a late onset of reproduction, a major reduction in spacing between births, and long productive and post-reproductive periods. The feeding niche exploited by humans evolved in tandem with these life history changes. It stressed nutritionally dense, hard-to-acquire foods whose acquisition relies on a wide variety of skills-based performances.

The human adaptation is in one sense both broad and flexible, and in another sense very narrow and specialized. It is broad in the sense that as hunter-gatherers, humans have existed successfully in virtually all of the world's major habitats. This has entailed eating a very wide variety of foods, both plant and animal, both within and among environments. It also has entailed a great deal of flexibility in the contributions of different age- and sex- classes of individuals. The relative contributions of men and women to food production appear to vary from group to group, and even the contribution of children and teens to food production varies predictably with the abundance of easy-to-acquire foods.

Our adaptation is narrow and specialized in that it is based on a diet composed of nutrient-dense, difficult-to-acquire foods and a life history with a long, slow development, a large commitment to learning and intelligence, and an age profile of production shifted towards older ages. We do not expect to find any human population that subsists on leaves or other low quality foods, or even fruits for that matter. We rather expect humans to remain at the very top of the food hierarchy in every environment they live in (humans often exterminate all other top predators in their habitat). This dietary commitment is reflected in the extremely reduced size of the human hindgut. Humans ingest foods that are already high quality and do not require much digestive work of detoxification. They also use their great intelligence to extract and hunt those foods. In order to achieve this diet, humans are very unproductive as children, extremely productive as adults, have very costly brains, and engage in extensive food sharing both within and among age- and sex- classes of individuals.

Meat plays a special role in the evolution of human diet and behavior. It is complementary to plant foods in that it provides essential macronutrients. It is energy-dense and comes in easily divisible, large packages, which lays a foundation for food-sharing and the division of labor (Lancaster & Kaplan, 1992; Lancaster & Lancaster, 1987). It cannot be readily obtained by juveniles, because it requires learned skilled performances, nor by reproducing women, because its attainment usually involves

risk and costs to infant care. Of all types of nutritional sources, meat is the only one that can lead to surplus production through the employment of skill and cannot be readily obtained by juveniles and women under most ecological circumstances. The original division of labor in humans between male hunting and risk taking and female gathering and care of offspring rests on its unique characteristics.

The theory and the data we presented suggest that the human life-course is based on a complex set of interconnected time-dependent processes and a co-evolution of physiology, psychology and behavior. There appears to be a tight linkage among the ordering of major psychological milestones (language learning, understanding and mastering the physical, biological, and social environment), the timing of brain growth, growth rates during childhood and adolescence, developmental changes in survivorship, behavioral, psychological and physiological changes with the transition to adulthood, profiles of risk with age, and rates of senescence and aging. It is very likely that a species-typical lifecourse evolved in response to the demands of a hunting and gathering lifestyle that was broad and flexible enough to allow successful exploitation of the world's environments, but specialized towards the acquisition of learned skills and knowledge to obtain very high rates of productivity later in life.

ACKNOWLEDGMENTS

The authors wish to express their appreciation to K. G. Anderson, John Bock, Michelle Cristiani, Sharon Pochron, and Troy Tucker, who helped with the preparation of tables and figures and with bibliographic research.

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Chapter 3

CULTURES AS SUPRAORGANISMAL WHOLES

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ABSTRACT

What do we mean by culture? This question has much in common with some that have been asked in the philosophy of taxonomy. The idea that species are not kinds of organisms, but rather wholes composed of organisms, suggests that cultural units may likewise be wholes made up of parts. If so, they are individuals rather than classes in an ontological sense. There are some very strong analogies between biological species and certain cultural units, especially languages. But there are also important differences, and identifying the wholes and their parts can be difficult. This contribution explores some of the possibilities, especially the relation of compatibility among the parts.

1. INTRODUCTION

A major task for the philosophy of science is to explain the meaning of theoretical terms. Although all of us can recognize behavior when we observe it, defining the term "behavior" is by no means an easy task. In

Perspectives in Ethology, Volume 13: Evolution, Culture, and Behavior
edited by Tonneau and Thompson, Kluwer Academic/Plenum Publishers, New York, 2000

addition to such semantic issues, there are ontological ones as well. What are the basic units of behavior, if indeed there are any? Is there such a thing as "a behavior?" The term "culture" is if anything even more difficult. Like behavior, culture is not something that is tangible. We cannot pick it up or weigh it, although we can pick up and weigh a vase or other product of culture. But culture also exists at a higher level—a level in a so-called hierarchy in which behavioral things occupy lower levels. The present essay is mainly concerned with what culture is, and peripherally with such related topics as what its components are.

The classical definition of "culture" in its anthropological sense that was provided by Tylor (1871, p. 1) may serve as a convenient starting point:

> "Culture or civilization, taken in its wide ethnographic sense, is that complex whole which includes knowledge, belief, art, morals, law, custom, and any other capabilities and habits acquired by man as a member of society."

The fundamental terms in a science can rarely be defined in just a few words, and Tylor's effort was hardly intended to be complete. Culture, he says, "includes" capabilities and habits, but does it include anything else? Are the persons who participate in the culture included therein? And by "art" does Tylor include the artifacts? Culture is acquired by man, but could organisms of other species acquire it? It is acquired as a member of society, but could it be acquired otherwise? The claim that such things are acquired suggests that they are not inherited, innate, or part of our genetic makeup. We may assume that one person passes such capabilities and habits on to another member of society through such mechanisms as teaching and imitation. They are transmitted, but not, as we would now put it, via the germ cells. We can also ask whether such transmission is defining of "culture" or just a characteristic feature (whether it is essential or accidental). We acquire knowledge and beliefs in our own life times. A person might even transmit knowledge to himself. The notion of somebody communicating with himself may seem odd, but that is precisely what we do that when we take notes in order to ease the burden on our memory. The idea that we cannot communicate with ourselves across time may reflect an implicit metaphysical assumption that the self exists only at the present moment. Accordingly one would not be the same person at different times. But organisms are individuals, and individuals change through time, so that the self remains the same thing, even though it may come to have quite different properties.

Such questions have been raised repeatedly, and of course there is a vast literature on how "culture" is, or might be, defined (recommended: Kluckhon & Kelly, 1945; Kroeber & Kluckhon, 1952; Cafagna, 1960; Weiss, 1973; Keesing, 1974; Durham, 1991). Herein I shall address several of the important issues in passing, but my basic concern is with what Tylor calls

"that complex whole." For it suggests that our recent progress in solving what has traditionally been called "the species problem" might make it easier to cope with analogous problems with respect to culture (Ghiselin, 1997).

2. INDIVIDUALITY

Initially, the "radical solution" (Ghiselin, 1974a) or "individuality thesis" arose as a response to the "nominalistic" claim that species are classes, or abstractions. Whether or not we should embrace nominalism and deny that classes are "real," there seems to be a good point here; only concrete, particular things (individuals) such as organisms can participate in processes. And if species were abstractions it would make no sense to say that they can do anything, such as evolve. Because species do in fact evolve, the claim that they are classes has to be rejected in favor of their being concrete, particular things. It follows that biological species are, ontologically speaking, individuals in the same fundamental sense that organisms are, and that organisms stand to species as parts to wholes, not as members to classes. Much as an organism is a group of cells and other parts, a species is an individual of higher, in this case supraorganismal, order than its components. Furthermore, species are not kinds, either of organisms or of anything else, and a species, like an organism, does not have instances. (Just as my left hand is not a Michael Ghiselin, I am not a *Homo sapiens*.)

Organisms are obviously material beings and tangible objects, but although all tangible objects are individuals, not all individuals are tangible. All individuals have definite positions in space and time and have a beginning and an end; more technically speaking, they are spatio-temporally restricted. A particular event, such as World War II, qualifies as an individual too. Although that event was not a tangible or substantial (material) entity it was spatio-temporally restricted. Cultural and behavioral wholes and their parts also qualify as individuals. This sentence is an individual sentence, and therefore an individual. It is also a part of a larger individual, this individual paragraph.

Tylor refers to culture as "that complex whole"—suggesting that it is one, and only one, individual. One might indeed want to interpret culture that way, perhaps treating the totality of culture as if it had evolved together with our species. Something of the sort is implied by Durham's (1990) conception of cultural evolution. He posits a common ancestral culture from which all cultures have descended. Evolutionary culture theory is then a kind of phylogenetics. Although the cultures that represent branches of a

phylogenetic tree are individual cultures, there is another individual of higher order that is the entire tree. One might want to call that historical entity culture in a broader sense, perhaps capitalizing it so that Culture is obviously a proper noun. Under this interpretation, Culture would be like Life, in the sense of the common ancestor of living beings on this planet and all of its descendants, and cultures would be like biological species. Whether we apply the notion of individuality to all these levels or not, anthropologists have been quite favorable to the idea that a particular culture is an individual (Marks & Staski, 1988).

"Species" is an equivocal (ambiguous) term that is rendered all the more confusing by the plural and singular form being identical. For example, when somebody refers to a "species definition" it could mean a definition of a class, namely the species category, and therefore a definition of species in general. But it could mean the definition of the name of an individual, in other words a particular species such as our own, *Homo sapiens*. In fact, the names of individuals (proper names) are "defined" in a way that many logicians prefer not to treat as definition at all. The properties that characterize individuals are not logically necessary for the names to apply, but at most provide descriptive information that may be useful in identifying the bearer of the name. So although all the human beings whom I have met are featherless bipeds, it would be wrong to treat a feathered mutant as if it did not belong to our own species.

"Culture" is in some ways even worse than "species" with respect to equivocation. Quite generally, "culture" is treated as a so-called "mass noun." Like "ice" it does not refer to a definite piece of matter or a unit of some non-material entity. (Even though we talk about individual ice-cubes, a cube of ice is not an ice, but some ice.) And "culture" taken as a mass noun basically means the entire class of entities cultural. So that would include the (individual called) Culture mentioned above, the class of cultures (with its individual members such as Maya culture), subcultures and sub-subcultures, anything else that exists as a component of a culture, and indeed just about anything that gets transmitted along lines suggested earlier. At the conference in Guadalajara at which this paper was first presented, somebody asked whether a group of musicians "possesses" culture. Given the various ways in which the term "culture" is used, it surely makes sense to answer that in one sense or another it does, but for that very reason the answer is not very informative.

3. HIERARCHY

We shall return to such analogies or equivalences among taxonomic units in due course. But before doing that we need to discuss the logic and

metaphysics of hierarchy. Hierarchies are characterized by two fundamental characteristics: levels, and entities that occupy, or are ranked at, those levels. There is a relation of *subordination* between the entities ranked at different levels: an entity at a lower level is subordinate to an entity at a higher one (and coordinate to entities at the same level). The entities in question can be individuals or classes, and there can be various relationships between the entities that are ranked at different levels. Behavioral scientists are familiar with a good example of a purely subordinative hierarchy in which the individuals all have different ranks: the well-known "pecking order" among fowl. A hen at a lower level is subordinate to, but neither part of, nor an instance of, a hen at a higher level. Here only one individual occupies each level.

Academia is partly organized into purely subordinative hierarchies. For example, the levels of freshman, sophomore, junior and senior are occupied by individual students. More than one individual occupies each level. There is no class inclusion relationship between those individuals, say, between sophomores and freshmen: it is not the case that all freshmen are sophomores. Nor is there a whole-part relationship between the individuals at different levels: it is hard to imagine what it would mean for a freshman to be part of a sophomore.

Inclusion and whole-part relations do exist in academia. The class of freshmen is included in the class of undergraduates and in turn in the class of students. The individuals are instances of the classes that are included in classes at higher levels. All freshmen are undergraduates and all undergraduates are students. Hence we may speak of an inclusive hierarchy. In addition there are incorporative (or whole-part) hierarchies, a good example of which would be Harvard University, which is composed of departments, which in turn are composed of professors. Here the levels are all occupied by individuals, and the individuals are parts of individuals at higher levels. Note however, and this is fundamental, that the parts are not instances of the wholes. We would not say that all Harvard professors are Harvard Universities!

For completeness we should observe that the individuals that have the same rank in a hierarchy are members, and therefore instances, of the same class. Thus, Harvard University is a university, and its Department of Psychology is a department. The more incorporative wholes that occupy the higher levels are concrete, particular things, whereas the levels themselves are abstractions, or classes.

In biological systematics as currently understood, we have a fairly straightforward incorporative hierarchy with individuals that are incorporated in other individuals, and with the same individuals also being members of classes or if you prefer occupants of levels, which are technically called "taxonomic categories." The individuals, which are taxa such as Chordata and Arthropoda, are each supposed to occupy a single level in

the system, in other words to be members of one and only one taxonomic category such as the phylum. We should mention that different classification systems may assign the same individual to different taxonomic categories; sometimes, for example, Arthropoda is treated as a superphylum instead of as a phylum.

The whole-part or incorporative hierarchy that is represented by formal plant and animal taxonomy can be extrapolated downward to the level of the organism and even lower, so that species and subspecies are composed of organisms, organisms of cells, cells of molecular wholes such as genes, etc. However, things become messy at and below the organism level. Not all organisms are parts of biological species; some of them are parts of asexual clones. This bothers some people, even those who are perfectly aware that not every atom in one's body is part of a cell. Less often recognized, though perhaps more disconcerting, is the fact that not all the components of species are organisms—unless one wants to define "organism" so that even zygotes and gametes are organisms. People want "*Homo sapiens*" to be a synonym for "human being" but it is not. Each of us is rather an organism-level component of *Homo sapiens*, just as a Harvard professor is an organism-level component of Harvard University, not a Harvard.

4. ABSTRACTION

Individuals are concrete, whereas classes are abstract. As we pass upward from lower to higher levels in an incorporative hierarchy, we go from the more particular to the more general. Thus Harvard University is more general than any of its individual departments or professors. But Harvard University and its departments and professors are concrete, rather than abstract (at least in the sense that I am using these terms here). Inclusive hierarchies are another matter. As one goes upward the entities become both more general and more abstract. Student is more abstract than freshman. Again, only concrete, particular things can do anything or participate in processes. An individual student can enroll in an individual university, but the very idea of student in the abstract enrolling in university in the abstract makes no sense at all.

Not being an historian of anthropology, I cannot say how much confusion has resulted from the notion that culture is an abstraction. There is of course a legitimate distinction between culture in the abstract and culture in the concrete, analogous to that between the phylum and Chordata, or between the organism in general and yourself. Nonetheless some statements in the anthropological literature would seem to indicate, if not a

belief that cultures and their parts are abstractions, at least a failure to think clearly about the ontological issues. Firth (1957) for example opposed the realism of Malinowski, insisting that cultural entities are abstract. On the other hand White (1959, 1975) rejected nominalistic views of cultural systems. Perhaps the habit of treating culture as if it were something "essentially mental" results from, or even causes, such confusion. A related metaphysical issue is whether it has to be something of the sort, but "behavioral" rather than mental. There is no good reason why individual events, whether mental or otherwise, should be considered abstract rather than concrete. If I encounter a shark when diving, I experience fear in the concrete because one concrete organism might take a concrete bite of another concrete organism.

5. LANGUAGES

Languages evolve very much as species do, and similarities between the two are most striking (Schleicher, 1869; O'Hara, 1996). A great deal has been written comparing species with languages, and the fact that languages and their components are individuals has often been recognized, implicitly if not explicitly. The problem of which levels to treat as equivalent has been somewhat more difficult to solve than one might think. On the face of it, the languages of individual persons, which are technically referred to as idiolects, are equivalent to organisms, and likewise dialects to subspecies, languages to species, and language families to the supraspecific taxa such as genera and orders. The populational character of subspecies and species on the one had and dialects and languages on the other provides an obvious and strong analogy. Likewise there is a striking resemblance between languages and species in their general tendency to evolve separately from one another. Above the species level and the language level we have what are basically "historical entities" that share a common ancestry but are not "cohesive." Even the fact that a certain amount of gene flow can occur between species strengthens the analogy, when we realize that words can be borrowed while the grammatical structure of each language maintains its autonomy.

Languages vary a lot from one place to another, much as species do. Being lineages that evolve, both languages and species can change to an indefinite extent yet nonetheless remain the same individual. Unless a language or a species splits into distinct lineages, it does not become two different things. Therefore the division of English, say, into Old, Middle, and Modern English does not individuate separate languages, but rather something like the childhood, adolescence and maturity of an individual human

being. Analogously, a so-called "chronospecies" is just a temporal part of a single, continuous lineage. It is curious that one philosopher treats this "cladistic" view of languages as if it were an *ad hoc* effort to justify the individuality of species, rather than compelling evidence in favor of it. Stamos (1998, p. 464) says, "it seems to me that few outside the modern species problem would wish to defend a *cladistic language concept*, in other words the position that a language which undergoes 'infinite evolution' is numerically the same language throughout. . . ." This struck me as rather surprising, for I had quite the opposite impression. In addition to refreshing my memory with respect to what I had read, I got on the Internet and put the question of a cladistic language concept to a group of 438 historical linguists. I did not get many replies, but they were emphatic and unanimous. The cladistic concept is the consensus position among linguists, and it has been so for more than two hundred years. Not only that, they do not even consider it an interesting issue, nor is it something that they debate among themselves. To the practitioners of historical sciences such as linguistics and phylogenetics the lineages are the obvious and fundamental reality. Treating their stages as if they were a succession of different things at different moments is to deny that very historicity and treat evolution as if it did not really happen.

Some authors have preferred to compare languages to organisms rather than to species. There is an ancient tradition of comparing all sorts of supraorganismal wholes, including species, ecological communities, and sundry political units to organisms (often calling them superorganisms). Culture is no exception (Weiss, 1973). Such "holism" has of course led to many misinterpretations of the entities thus analogized, and overestimating the power of group selection is only one example (Ghiselin, 1974b). And when we push the analysis below the level of the organism and the idiolect we may find ourselves hard-pressed to decide what the equivalent functional units might be. Attempts to find linguistic equivalents for genes and chromosomes are apt to be all too facile, and misleading to boot. (There is to my knowledge nothing like a haplo-diploid language, for example.)

Then there is the question of what qualifies as a component. In dealing with species, organisms, and the parts thereof we are concerned with substantial wholes made up of lesser substantial wholes, and in that respect each whole is rather like a machine with its parts. The problem of identifying components has not bothered anatomists very much. Whether secretions are part of the body is hardly a burning issue with them. In the case of social units such as clubs, the organisms can again be treated in a straightforward manner as substantial components of substantial wholes. With respect to languages, however, we make a distinction between the linguistic community on the one hand, and the language itself. These supposedly are different things, and that makes sense insofar as the speech is not the

speakers, just as a dance is not the dancers; they fall under different ontological categories. But what is the relationship between the activity and the participants who "take part" in it? And should we interpret "language" to mean the activity, or perhaps something else, such as the conventions according to which it is conducted? In that case we would say that language is a group of rules employed in discourse, and analogous suggestions have been made that other social entities—institutions such as law for example—"are" rules.

To be sure, all sorts of things have rules, and rules are entities in their own right. But having rules or following rules is not the same thing as being rules. A club may impose rules upon the conduct of its affairs, but it may be quite free to change those rules, for example by amending its constitution, and yet obviously remain the same club. With games, perhaps, we are more apt to feel that if the rules are changed it is a different game. But this would be a non-evolutionary way of looking at things. When we speak of a body, or *corpus* of laws, the metaphor suggests that we recognize a complex whole (again) which, like an organism (again), is an individual, the components of which are themselves individuals. Obviously, the whole can be changed by adding, deleting, or modifying parts, and yet remain the same particular thing.

If we want to treat language as a corpus of rules, we had better avoid doing so in a simplistic fashion, and not reduce it to a sort of glossary and a grammar. Language intimately coexists with the rest of our lives, including what we talk about. Literary allusions provide an obvious link to something beyond the dictionary. If the literature in a language is in no sense a part of the language itself, then perhaps we need to recognize some larger whole of which both are components. One way or another we also have to accommodate the speakers and the hearers, the writers and the readers. How about the books and manuscripts? They exemplify what is often called "material culture"—artifacts in general. Some authors include artifacts as parts of culture (D'Andrade, 1995). Alternatively such artifacts as may be considered products, rather than parts, of culture. And yet with respect to literature, we might prefer to treat the authors as active participants and the books that they write as passive ones. Likewise paintings are studied, imitated, and copied by the artists who paint them.

6. A PROCESSUAL SOLUTION

Let us now consider how cultures might be treated as evolutionary units along lines that I have elsewhere suggested for species (Ghiselin, 1997). Taking a processual point of view, we might treat a culture as a

supraorganismal whole that is composed both of activities and dispositions to engage in such activities, with organisms (people) as actors or participants, and with rules or conventions that govern what those activities are and how they may be carried out. The notion of a supraorganismal whole may seem a bit forced here, because it would be a whole made up not of organisms, but of what the organisms do and how they do it. The organisms do participate in culture, however, and their communal activity produces something that is populational, or emergent. The participants have access to more than just their own capacities. There is more to the vocabulary of a given language than just a single person's idiolect, just as the gene-pool of a species contains more alleles than does a single organism's (diploid) genome. Likewise, if we recognize the existence of a "culture pool" then it makes sense to say that artifacts are parts of it, though perhaps we might want to consider them repositories.

But then again genetical variation within species is held within limits by natural selection. Within-species homogeneity is particularly obvious with respect to chromosome numbers, and the reason has to do with the *compatibility* that the component organisms must possess if they are to function as effective participants in a reproductive community. Such compatibility is a necessary condition for the interactions that go on in such processes as mating, fertilization, meiosis and embryogenesis. The "dance of the chromosomes" is an apt metaphor, for it suggests the coordinated interaction among parts that we observe in a *pas de deux*. Furthermore, there is nothing "sacred" about the particular rules that are followed; genetic systems evolve and so do cultural entities. The rules can change, but only if the compatibility among the parts is maintained. Under ordinary circumstances, there are no saltations in either organic or cultural evolution. (Allopolyploidy, in which a species originates by incorporation of complete chromosome sets from two distinct species, might be considered an extraordinary circumstance.)

"A" culture, then, is a nexus of activities together with dispositions that affect how those activities are carried out, and with participants that have the capacity to act in concert with one another, and in so doing to share and exchange cognitive resources via extrasomatic channels of communication. This formulation is too abstract except as a summary and first approximation, so I hasten to expand and qualify. We need to distinguish what goes on within cultures from what goes on within species, hence "extrasomatic" transmission. "Cognitive resources" is about as general a term as I could think of for what does get exchanged, shared, transmitted etc.; we need a very broad term that expresses everything from the moral of a story to a skill or habit acquired through imitation. Perhaps for an audience of psychologists, the term "cognitive" is apt to be misleading, and one might prefer a behavioral equivalent. There is a problem insofar as other

resources, such as goods and services, do get exchanged during the activities in question. Also, some would question whether, say, an aesthetic message is a resource, though I at least would have no problem with that. What one does about deceptive messages and the like is a problem that I would rather just mention. Having the *capacity* to act in concert is not the same thing as *actually* doing so, though it is a necessary condition. Mentioning that explicitly makes the parallel with the biological species definition, with its "potential interbreeding," somewhat more obvious. The term "disposition" may seem a bit vague, but again we need something very general, to include perhaps everything that Tylor had in mind in the above quotation when he enumerated customs, capabilities, and habits.

The focus upon resources is important here because a bioeconomic perspective helps us focus upon the ontologically significant issues. Sociobiologists especially have made some claims that seem odd, but for reasons that are hard to articulate. Species and cultures are (among other things) instrumentalities by means of which organisms gain access to the resources that they use in competing with other organisms. It is by virtue of their quality as resources that chromosomal deletions, whether selfish or not, get removed from genomes. It is by virtue of their quality as resources that we either do or do not try to remember telephone numbers and other selfish memes, or even throw away whole books full of them. Granted, according to one metaphysical perspective, when I write down my telephone number and give you the copy that I have made, we are supposed to call the thing that has been passively replicated the "replicator" rather than the active agent which does the replication. Use of the ending "-or" for something that is not an agent is incompatible with the fundamental syntax of English and Latin, and serves to bolster the metaphysics at the cost of clear thinking and communication. According to another, and I daresay more enlightening, metaphysical perspective the reason why I actively replicate the telephone number is that I gain an economic benefit from providing you with it. The interactors (see Hull, 1988a; Heyes & Plotkin, 1989), not the so-called replicators, are the economic agents (Ghiselin, 1997).

A language would seem to fit the definition of a cultural whole, and the definition of culture here proposed would seem to provide a reasonably accurate characterization of languages as well as of cultures in a somewhat broader sense as incorporating that which anthropologists generally consider the components of the culture of a group of people: customs, mythology, and cuisine for example. Obviously one can characterize the populace of a given village on the basis of the cultural wholes in which they participate, such as their language and their religion. But the various wholes in which they participate are not always coextensive. Their religion, for example, may be more widespread than their language. Some persons are bilingual, participating in more than one such (cultural) whole. If languages,

like species, can be characterized as higher-level units that are sufficiently closed that they evolve independently of other such units, this is not necessarily true of all cultural wholes. Concerted evolution among various sectors of culture is more than just a theoretical possibility. Law, ethics, and religion obviously have tended to co-evolve. Given the structure of the cultural world, it seems unlikely that we will ever come up with a satisfactory definition of a higher-level category called "culture," the members of which are really equivalent and commensurable when ranked at that level.

Cultural wholes may or may not be subdivided in a manner that has some parallel within biological populations. There are sub-populations within species, almost exclusively differentiated on a geographical basis, that are comparable again to dialects within languages. But the division of labor within species, whether it involves sexual dimorphism, castes in social insects, or just about anything else, is not based upon separate genetical populations. Likewise the division of labor within human society definitely is accompanied by the formation of social organizations that form distinct sub-cultures that coexist locally. The proliferation of specialized vocabulary and jargon within trades and professions is a most conspicuous symptom. There are good reasons why some professions tend to be practiced by persons of a particular ethnicity. Trading networks set up by minority ethnic Chinese provide a particularly good example of how this works (Landa, 1994). The traders derive an advantage from dealing with those whom they can trust, and that means other Chinese who share their beliefs and customs. One might take this as an example of culture interacting with the economic system, and that is a perfectly legitimate point of view. On the other hand one might equally well insist that culture exists by virtue of its economic advantages. The participants in a given whole are enabled to interact more effectively, especially when sharing and exchanging various resources; it does not matter whether these resources be material, cognitive, or aesthetic ones. Whichever view we take, it is part of the overall picture. Whether the resources be genetic or cognitive, the various systems do not evolve in different worlds (Lumsden & Wilson, 1981; Plotkin & Odling-Smee, 1981; Staddon, 1981) and they all have an economic aspect (Boyd & Richerson, 1985).

7. THE CULTURE OF SCIENCE

Science is sometimes given as an example of culture or perhaps a culture with more or less distinct subcultures, and even as something that evolves very much like biological species (Hull, 1988b). The subculture or institution that we call science has been set up, to some extent consciously,

so as to make it cosmopolitan in scope and thereby have it transcend the limitations of nationality, language, and local culture in general. The efforts initiated by Linnaeus to create a uniform procedure for classifying and naming groups of plants and animals provide good examples. The use of Latin or latinized binomials rather than vernacular terms had various advantages, but mitigating national rivalry was certainly a significant one. The formulation of an International Code of Zoological Nomenclature and the establishment of an International Commission on Zoological Nomenclature likewise made it easier for persons of diverse nationalities to work together harmoniously toward common ends. However the botanical and the zoological codes, although similar in their more important respects, are nonetheless quite separate, and efforts to establish a single code for taxonomy as a whole have thus far failed. So parochiality among systematists results from, and perhaps reinforces, the division of labor along taxonomic lines. One might assume that cultural diversity, like species diversity, is always a good thing and that it ought to be preserved and even fostered. But our example suggests that the topic is more complex. Nobody would deny the advantages to specialization and the division of labor on the part of the scientists who devote their careers to the study of organic diversity. But the specialized subunits are supposed to function as part of a larger functional whole. Compatibility within the subunits by no means necessitates that there will be compatibility between them.

In addition to possible incompatibilities between systematic zoology and systematic botany, there can be incompatibilities between systematic biology and the rest of science, and indeed with the entire gamut of cultural wholes. One consequence of having life on earth be broken up into species is that it enables populations of organisms to diversify indefinitely and become very different from one another. Speciation results from the elimination of reproductive compatibility, leading to reproductive isolation between populations, and thereby permitting such divergence. Within culture or civilization the units can diversify without having to be isolated. Indeed the basic advantage to having a culture at all is that the parts thereof are by no means isolated from one another, and therefore the advantages of communication and other modes of interaction can be realized.

Lately quite a number of philosophers have argued for what is called "pluralism" or the "disunity" of science (Dupré, 1993; Rosenberg, 1994). There is some merit to what they say, given the philosophical tradition in which they continue to operate. The older positivistic tradition that has largely been superseded sought for unity among the sciences through a reductionist program, such that everything could ultimately be cast in the language of physics. Biologists of course are interested in what goes on at higher levels, and in the history of events and processes that go on at those levels. An excessively monolithic view of things is of course apt to leave out

the rich diversity that characterizes the living world and of the systems of knowledge that are supposed to provide us with an understanding of that diverse world. But richness of content is by no means incompatible with the sort of integration that characterizes an organic whole. The individuality thesis allows us to interrelate the various branches of knowledge and to appreciate the unity that exists at its roots.

ACKNOWLEDGMENTS

Both François Tonneau and Nicholas Thompson provided detailed criticism that greatly improved the original manuscript. Since the advice was often heeded more in the spirit than the letter the usual disclaimers about responsibility for the final version are especially applicable. My thanks also to our hosts at the Guadalajara meeting, and to the participants for much lively discussion.

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Chapter 4

NICHE CONSTRUCTION AND GENE-CULTURE COEVOLUTION: AN EVOLUTIONARY BASIS FOR THE HUMAN SCIENCES

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ABSTRACT

Traditionally evolutionary theory treats the adaptations of organisms as consequences of a process whereby natural selection moulds organisms to fit pre-established environments. The changes that organisms themselves

Perspectives in Ethology, Volume 13: Evolution, Culture, and Behavior
edited by Tonneau and Thompson, Kluwer Academic/Plenum Publishers, New York, 2000

cause in their own environments are seldom through to be evolutionarily significant. However, active organisms partly create their own selective environments by "niche construction," and ancestral organisms can pass on legacies of modified natural selection pressures in their environments to their descendants. In this chapter, we build on conventional evolutionary theory by adding niche construction. We argue that the resulting enhanced theory of evolution provides a better basis for understanding how human cultural processes interact with human genetic processes in human evolution, and we discuss how human cultural niche construction may have co-directed, and may still be co-directing, human genetic evolution.

1. INTRODUCTION

In this essay we want to reopen the issues of how human cultural processes relate to the processes of human genetic evolution, and how these two sets of processes interact with each other. In revisiting these issues we will introduce two new concepts, and then explore the extent to which these new concepts may change some previously held assumptions, and some previous approaches. The new concepts are those of niche construction, and ecological inheritance. Niche construction refers to the modification of the environments of populations by the activities of phenotypes. On the evolutionary time scale, it is the equivalent of what Jones, Lawton, and Shachak (1997) call "ecosystem engineering" in ecology. Ecological inheritance refers to the passing on of legacies of phenotypically modified natural selection pressures by ancestral organisms to their descendants (Odling-Smee, Laland, & Feldman, 1996).

We will first demonstrate how adding niche construction and ecological inheritance to contemporary evolutionary theory enhances and extends the theory of evolution itself. Then we will consider how such an enhanced theory of evolution may change our understanding of the relationship between human genetic evolution and human culture, in the context of an overall gene-culture coevolutionary scheme which includes both niche construction and ecological inheritance. Here we will focus primarily on the consequences of human cultural niche construction, and consider how it may have modified some human natural selection pressures in the past, and may thereby have co-directed human genetic evolution. We will also consider briefly the possible relevance of the same inclusive gene-culture coevolutionary scheme to some aspects of modern human life.

2. BIOLOGICAL EVOLUTION

Most biologists have been brought up with a particular understanding of how evolution works (Figure 1). Natural selection acts on populations of diverse phenotypes, and it influences which phenotypes survive, reproduce and pass on their genes to the next generation via genetic inheritance. Adaptation is regarded as a consequence of this process, achieved by natural selection moulding organisms to fit pre-established environmental templates (Burian, 1992). These "templates" may be dynamic, because processes that are independent of organisms cause changes in the environments to which organisms adapt (Van Valen, 1973). However, the changes that organisms bring about to their own environments are seldom incorporated in evolutionary theory.

This traditional understanding largely ignores the feedback in evolution due to the modification of natural selection pressures by active phenotypes. Through their metabolisms, their behaviour, and their choices,

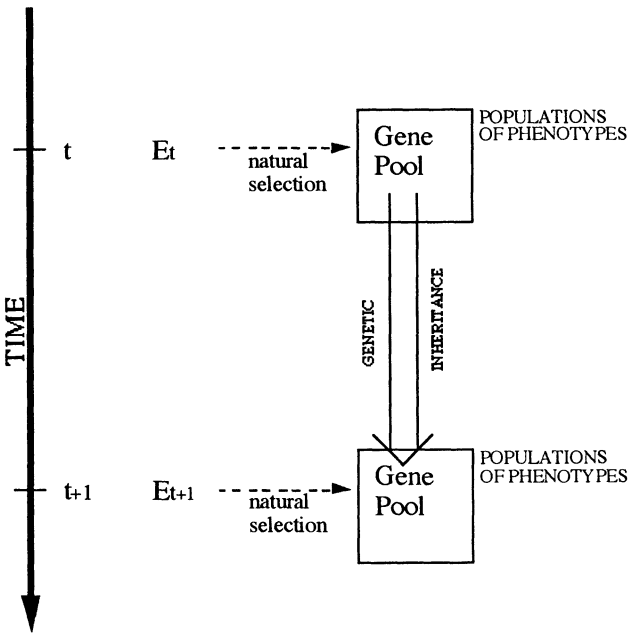


Figure 1. Standard evolutionary theory. Populations transmit genes from one generation to the next, via genetic inheritance, under the direction of natural selection (t = time; E = the selective environment).

populations of organisms partly define, partly create, and partly destroy their own environments (Jones, Lawton, & Shachak, 1994, 1997); in doing so, they modify some of the natural selection pressures in both their own and in each others' environments (Lewontin, 1983). Biotically-modified natural selection pressures may then feed back to those same populations, where the result may be selection for genotypes different from those selected previously. Hence, adaptation cannot occur exclusively relative to pre-established selective environments, as evolutionary theory currently implies. Instead it must occur relative to selective environments that have themselves been partly transformed by the prior activities of contemporary and ancestral organisms.

Elsewhere we have called the environment-modifying activities of organisms "niche construction," with the proviso that niche construction can be either positive or negative (Odling-Smee, 1988; Odling-Smee, Laland, & Feldman, 1996; Laland, Odling-Smee, & Feldman, 1996). Niche construction is positive when it increases the fitness of the niche-constructing organisms themselves, and it is negative when it decreases their fitness. In the short run, niche construction is expected to be positive since most organisms usually act in ways that are, on average, immediately adaptive. In the longer run, however, niche construction may be either positive or negative; organisms sometimes spoil their own niches.

The best way to illustrate what we mean by niche construction is with examples. The first example, concerning the activities of earthworms, was originally provided by Darwin (1881). Through their burrowing activities, dragging organic material into the soil, mixing it with inorganic material, and casting, earthworms can dramatically change the structure and the chemistry of the soils in which they live (Lee, 1985). Hence, as a result of the cumulative effects of past generations of earthworm niche construction, contemporary earthworms live in radically altered worlds where they are exposed to natural selection pressures that have been considerably modified by their ancestors.

A smaller scale example is provided by the hygienic behaviour of honeybees. Honeybees construct their combs out of wax, and then use the cells they have constructed for rearing offspring, and for storing honey and pollen. One of the duties of worker bees is to uncap sealed cells containing dead pupae and to remove the dead from the hive. Rothenbuhler (1964) showed that these uncapping and removal behaviours are strongly influenced by genes, selection of which could have been a consequence of the activities of other members of the hive. Thus, contemporary genetic variation is presumably influenced by a history of selection pressures that have resulted from the changing hives and the combs built for many generations by bees.

A third example is a case of human cultural niche construction due to agriculture. It concerns the enzyme lactase which degrades lactose and

is necessary for the digestion of milk. In most mammals lactase is synthesised by infants, but not by adults. However, when our human ancestors domesticated cattle, they modified a natural selection pressure in favour of genes which enable lactase to be synthesised in adults (Bodmer & Cavalli-Sforza, 1976; Feldman & Cavalli-Sforza, 1989). Today between 70% and 100% of human adults who come from areas with a long history of dairy farming are lactose tolerant, while the majority of human beings from other areas are not. Durham (1991) recently pointed out that this story is more complicated than was originally thought because it also involves calcium absorption, latitude, sunlight, and vitamin D deficiency; but the overall observation remains the same.

These three examples of niche construction, and many others like them, are already well known to evolutionary biologists. Before going any further it is therefore worth considering how contemporary evolutionary theory currently deals with them, and why the evolutionary feedback they illustrate is not already adequately handled by this theory.

Dawkins (1982, 1989) partly recognised the role of niche construction when he pointed out that genes in organisms not only express phenotypes, but also frequently express "extended phenotypes," which reach out beyond the bodies of the organisms themselves to affect components of the organisms' environments. For example, Dawkins argues that the lodges, lakes and dams built by beavers are "extended phenotypes" of beaver genotypes, which like some components of the beavers' bodies, their teeth or their tails for instance, must have evolved under the influence of natural selection.

Dawkins is clearly right, but he doesn't go far enough. When a beaver builds a dam it influences more than just the probability that the particular genotypes that underly its dam-building behaviour will be selected. The beaver's dam, lake and lodge are important components of the beaver's environment, so beavers are particularly likely to change the way natural selection may act on their populations by ensuring that modified selection pressures may eventually feed back to act on their teeth, their foraging behaviours, their reproductive behaviour, their susceptibility to disease, their social system, and so on. For instance, because they spend so much of their lives in water, partly as a consequence of their dam-building behaviour, beavers are particularly susceptible to tick infestations. This susceptibility appears to have led to the evolution of specialised tick extractors on beaver claws, and may also have led to an increase in social grooming (Hanney, 1975). The point that Dawkins overlooks is that "extended phenotypes" do not just affect the selection of those genotypes that are responsible for expressing the extended phenotypes in the first place. They are also highly likely to modify selection on phenotypes affected by other genetic loci, either in the same population, or possibly in a different coevolving population, for example, in the beavers' ticks.

This failure to acknowledge the full extent of the consequences of niche construction is typical in contemporary evolutionary theory. Examples of niche construction are ubiquitous, for instance in habitat selection, in frequency- and density-dependent selection, in maternal inheritance, and in coevolution. The phenomenon itself is therefore widely recognised. However, in each of these cases the theoretical treatment of niche construction has been quite limited. For example, theoretical treatments of habitat selection usually focus only on those genetic loci that directly affect the habitat choice itself, and do not consider other loci (e.g., Cody, 1981; Rosenweig, 1987; Jaenicke & Holt, 1991). The same is true of contemporary models of frequency- and density-dependent selection (e.g., Slatkin, 1979a, b; Endler, 1988). Some of the models of maternal inheritance go further by recognising a non-genetic inheritance system, the maternal inheritance itself, but they are usually limited to studying this phenomenon in only two successive generations (e.g., Feldman & Cavalli-Sforza, 1976; Kirkpatrick & Lande, 1989; Cowley & Atchley, 1992). Finally, contemporary coevolutionary models (e.g., Futuyma & Slatkin, 1983; Thompson, 1994) make little attempt to deal with cases where niche construction results in the modification of abiotic sources of natural selection in the environment (such as the soil or a water resource), in addition to biotic sources of selection in the form of the phenotypes of some other coevolving population. Such intervening abiota can be important because they can substantially influence the dynamics of populations (Gurney & Lawton, 1996). What we still lack is a body of theory that sets out to explore niche construction and its feedback on evolution in general.

2.1. Natural Selection and Niche Construction

We previously proposed a general theory of organism-environment co-evolution that explicitly extends the standard theory of evolution by treating niche construction as a general evolutionary process (Odling-Smee, 1988; Odling-Smee, Laland, & Feldman, 1996). The basic idea is illustrated in Figure 2.

Our claim is that this second, niche-constructed component of organisms' environments can generate a second inheritance system in evolution (Figure 2), one that Odling-Smee (1988) called an "ecological inheritance." An ecological inheritance comprises whatever legacies of modified natural selection pressures are passed on by ancestral organisms to their descendants, via their external environments, as a consequence of their niche-constructing activities. Important differences between genetic inheritance and ecological inheritance include that the former is transmitted internally, from only one (asexual) or two (sexual) parents, by reproduction, whereas

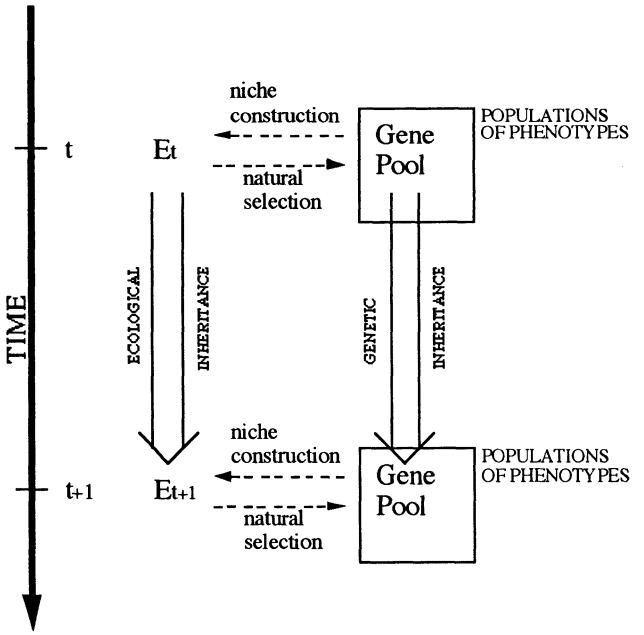


Figure 2. Standard evolutionary theory with niche construction and ecological inheritance added. On the right of Figure 2, genes are transmitted by ancestral organisms in generation t via genetic inheritance to their descendants in generation $t + 1$, subject to natural selection, exactly as described by standard evolutionary theory. However, on the left, selected habitats, modified habitats, and modified sources of natural selection in those habitats, are likewise effectively transmitted by these same organisms to their descendants via their local external environments, E, from E_t to E_{t+1}. The selective environments encountered by descendant organisms are partly determined by independent environmental events, in the manner described by standard evolutionary theory; for example, they could be determined by climate, by the weather, by other organisms, or just by physical and chemical events. However, they are also partly determined by ancestral niche construction.

the latter persists, or is actively chosen or maintained by one generation for the next, and is passed on via the external environment, possibly by many niche-constructing organisms rather than exclusively by parents (Odling-Smee, 1988; Odling-Smee, Laland, & Feldman, 1996). Niche construction is a second co-directing process in evolution, which in conjunction with natural selection, codetermines what happens to populations through cycles of natural selection and niche construction. The overall result is a dual-inheritance system between successive generations of populations; a genetic inheritance directed by natural selection, and an ecological inheritance directed by niche construction. Figure 2 depicts the sub-processes assumed by evolutionary theory after niche construction and ecological inheritance

have been added to it. Our proposal is that Figure 2 is a more realistic picture of what is happening in nature than standard evolutionary theory.

2.2. Amplification

When organisms modify their environments, their actions do not always have evolutionary consequences. For instance, if at any generation, the organisms in a population only modify their environments temporarily or inconsistently, or if the consequences of their environment-modifying acts are erased or overwhelmed by other independent agents in their environments, then there may be no modification of any source of natural selection in that population's environment. In this case there will be no ecological inheritance.

In contrast, niche construction can influence the evolution of a population even without generating an ecological inheritance, as happens when niche construction acts exclusively within single generations. For instance, individual web spiders repeatedly make webs in their environments. Subsequently, the consistent presence of a web in each spider's environment may, over many generations, feed back to become the source of a new selection pressure for further changes in behavior of the spiders. Specific examples include the attachment of a leaf or a twig by some spiders to their webs to make a refuge for themselves, or the building by a species of orb web spider, *Cyclosa*, of dummy spiders in its webs to divert the attention of predators (Edmunds, 1974). In these cases there is clearly no ecological inheritance between generations, because nothing is transmitted or persists from one generation to the next in the external environment. Spiders' webs could hardly be more transitory. They do not persist for generations. They are gossamer hanging in the wind, often subject to daily reconstruction. Yet the repeated construction of webs by each spider, in each generation, constitutes a form of repetitive niche construction that has likely been sufficient to modify some aspects of natural selection in these spiders' environments without the ecological inheritance of the webs themselves.

In more complicated cases, in addition to modifying their own environments, organisms may repeatedly modify their offsprings' environments. Here, the consequences of niche construction are "transmitted" from one generation to the next through the external environment, in the form of parentally modified natural selection pressures for their offspring. This transmittal is sufficient to establish a second inheritance system in evolution, an ecological inheritance (Figure 2). Offspring now receive a dual inheritance from their parents, their genotypes, and some parentally-modified sources of natural selection as a consequence of the parentally-changed environment.

The cuckoo is a two-generation example of both niche construction and ecological inheritance. Cuckoos are brood parasites in that cuckoo mothers repeatedly select host nests, such as those of pipits or warblers, in which to lay their eggs, generation after generation, deceiving the adults of these other species who raise the young cuckoos. Cuckoos thereby bequeath natural selection pressures to their offspring, in addition to naturally selected genes. For example, cuckoos have short incubation periods, leading to early hatching. These legacies of modified selection pressures have apparently selected for a variety of specialised adaptations in juvenile cuckoos, enabling them to cope with their adopted nurseries. For example, newly hatched cuckoo chicks throw out the still unhatched eggs, or young, of their hosts from the parasitized nests, thereby ensuring that they are raised alone. Subsequently, individual cuckoo chicks also make rapid begging calls that sound like a whole brood of their host's chicks, apparently to stimulate adequate caring responses from their hosts. Later, as adults, cuckoos that have been raised in the nests of particular hosts may preferentially parasitize the same hosts when they become parents, possibly having learned to do so through early imprinting (Krebs & Davies, 1993; Davies, Kilner, & Noble, 1998).

The effects of niche construction and ecological inheritance, however, are restricted neither to two generations nor to two parents, but may generalise to involve multiple ancestors and multiple generations. Earthworm niche construction, for example, typically leads to cumulative effects in the soils the earthworms inhabit over many generations. Earthworms can therefore pass on these progressively modified natural selection pressures in their environments, not just to their offspring, but to many generations of descendents.

2.3. Modelling Niche Construction

The capacity of organisms to modify their own selection, or that of subsequent generations, raises some new questions about the dynamics of evolution. The general effect of adding niche construction and ecological inheritance to natural selection and genetic inheritance is to introduce a phenotypically-driven feedback, that if included in evolutionary theory, is likely to change our understanding of how the evolutionary process works, possibly profoundly (Robertson, 1991). The extent of such changes can be discovered only by incorporating both niche construction and ecological inheritance into formal population genetic models of evolution. We have begun to do this using a branch of population genetics known as two-locus theory. We will not present our basic model here, since it has been fully reported elsewhere (Laland, Odling-Smee, & Feldman, 1996), but we will describe its logic and some results.

The model considered a single population of diploid individuals and focussed on two genetic loci, which we labeled **E** and **A**, each with two alternative alleles, *E* and *e*, and *A* and *a*. We made the following assumptions: (i) The population's capacity for niche construction is influenced by the frequency of its alleles at the first, or **E** locus. (ii) The amount of some resource **R** in the environment depends, either wholly or in part, on the niche-constructing activities of past and present generations of organisms, and therefore on the frequency of genotypes at the **E** locus. (iii) The amount of the resource **R** in the environment subsequently determines the pattern and strength of the natural selection that feeds back to act on the **A** locus.

These assumptions need qualifying. First, the hypothesis that niche construction is influenced by the **E** locus does not imply that we believe niche construction is a manifestation of a single gene. This assumption merely means that, to keep things simple, we initially focussed on only one of the many genes that might influence niche construction. Second, this model potentially generalises to other, more elaborate feedback cycles. For example, the **A** locus need not be in the same population as the **E** locus. The two loci could easily be in different coevolving populations (Futuyma & Slatkin, 1983; Thompson, 1994). Nor does **R** need to be a biotic resource. In principle **R** could be any environmental or ecosystem component, biotic or abiotic. For example it could be a food item, a parasite or a predator, or a water resource, detritus, a chemical element in the soil, or an inherited artifact such as a burrow or a dam. All that matters is that **R** is both a source of natural selection on the **A** locus, and that **R** can be modified by the niche-constructing activities of a population's phenotypes under the influence of **E** locus genotypes.

The results of this first model suggested that niche construction can indeed make a considerable difference to how populations evolve. For example, we found that modified natural selection pressures due to niche construction can sometimes override independent sources of natural selection, and drive populations along evolutionary trajectories alternative to those they would have taken if they had not expressed any niche construction. They can also initiate new evolutionary episodes by changing selective environments that would otherwise have remained unchanged. In addition, niche construction can influence the amount of genetic variation in a population by affecting the stability of polymorphic equilibria and generating new equilibria. Moreover, niche construction can generate unusual evolutionary dynamics. For instance, time lags were found between the onset of a new niche-constructing behaviour, and the response of a population to a selection pressure that was subsequently modified by the novel niche construction. These time lags generate an evolutionary inertia, such that unusually strong selection is required to move a population away from an equilibrium. They also generate a momentum, which causes populations to

continue to evolve in a particular direction, even after a selection pressure has changed or is reversed (for a more detailed account of these results see Laland, Odling-Smee, & Feldman, 1996). Thus, adding niche construction and ecological inheritance to natural selection and genetic inheritance can make a considerable difference to our understanding of how evolution works.

3. IMPLICATIONS OF NICHE CONSTRUCTION FOR THE HUMAN SCIENCES

Two aspects of niche construction are likely to be of particular interest to the human social sciences. First, because of niche construction, phenotypes play a second role in evolution. In addition to surviving and reproducing differentially and carrying genes across generations in response to natural selection, niche-constructing phenotypes co-direct their own population's evolution by changing some of the natural selection pressures that act on their own genotypes, and by bequeathing legacies of modified natural selection pressures to their descendants. Second, there is no requirement for niche construction to result directly from genetic variation before it can influence the selection of genetic variation. For example, niche construction can depend on individual and social learning, and in humans it can depend on culture. The latter dependence therefore raises the possibility that human culture may have played a significant co-directing role in the genetic evolution of our own species, by modifying human selective environments.

One example of learned niche construction in animals was reported in British blue tits. Partly guided by each other, these birds recently learned how to open the foil tops of milk bottles left by milkmen on peoples' doorsteps, and to gain access to a new resource, the milk (Fisher & Hinde, 1949; Sherry & Galef, 1984). The evolutionary consequences of this learned innovation are unknown, but it is possible that the exploitation of this new resource may now be selecting for a further evolutionary change in the blue tits, for instance, for a different digestive enzyme, or an improved learning ability.

An example of human cultural niche construction leading to an episode of human evolution may have occurred among the "Kwa-speakers" of West Africa. The Kwa-speakers are yam cultivators who for many generations have cut down trees in tropical rain forests to create clearings in which to plant yams. The clearings increase the amount of standing water in the environment, and provide better breeding grounds for malaria-carrying mosquitoes. That, in turn, intensifies selection for the

sickle-cell anemia allele because of the protection against malaria offered by this allele at the hemoglobin locus (in the heterozygotic condition). The central point here is that an observed increase in the frequency of the sickle-cell allele among the Kwa-speakers appears to have been induced by a human cultural activity, agricultural niche construction (Durham, 1991).

The ability of human culture to modify some human natural selection pressures introduces a new phenomenon in evolution that may be unique to humans. To the extent that any species' capacity for expressing niche constructing activities ultimately stems from its genetic inheritance, its ability to modify any natural selection pressure in its environment will be constrained, not only by the properties of whatever environment it is modifying, but also by the rules of its own genetic inheritance system. For example, in no such species will a new niche-constructing trait be able to evolve faster than the rate at which new genes can spread through a population, and this rate will be constrained by several factors, including the generational turnover time of the population. Hence, the capacity of any such population to modify any natural selection pressure in its environment by a niche-constructing activity that depends on its genes, will also be constrained by its genetic inheritance.

This pattern of constraint changes, however, in the case of human cultural niche construction. The human capacity for culture, including the human capacity for social learning and language, may still be a part of our own species-specific genetic endowment, but cultural niche constructing activities, unlike all other kinds of niche constructing activities, do not ultimately stem exclusively from the genetic inheritance system. Instead they also depend on cultural inheritance, which is not constrained by the same rules as those that apply to genetic inheritance.

For example, cultural inheritance is not Mendelian. It depends on the inheritance of "acquired characteristics" and is therefore quasi Lamarkian. Nor is culturally inherited information or "knowledge" an immediate product of natural selection. Rather it is the product of several different kinds of cultural selection processes as well as natural selection (Cavalli-Forza & Feldman, 1981; Boyd & Richerson, 1985; Durham, 1991). In addition, cultural inheritance does not depend on a maximum of only two parents, as does genetic inheritance, but it can depend on many more. Also cultural inheritance is not a discrete event which only occurs once per lifetime, at the moment of an organism's origin, but rather is a continuous process which may occur at any moment during an individual life. Finally, the modes of transmission of cultural inheritance are more varied than are the modes of genetic transmission. For example, human cultural inheritance may involve oblique and horizontal, as well as vertical modes of transmission (Cavalli-Sforza & Feldman, 1981; Aoki & Feldman, 1987), and even on occasions reversed transmission (from offspring back to parents) whereas,

apart from viruses and plasmids, genetic inheritance is transmitted from parents to offspring only, and is exclusively vertical.

These differences raise the possibility that hominid cultural niche-constructing activities, unlike all other kinds of niche-constructing activities, may partly escape from the constraints and limitations of the genetic inheritance system, and may principally be governed instead by the very different rules of cultural inheritance. The rules of cultural inheritance potentially allow novel niche constructing activities to spread far more rapidly in human populations via cultural inheritance, than would be possible if they depended exclusively on genetic inheritance. Thus, human cultural niche construction may have a unique capacity to modify natural selection pressures in environments at a much faster rate, and probably on a far greater scale, than anything that would be possible if human niche-constructing activities depended solely on genetic inheritance.

For example, if the appearance of a new human niche-constructing behaviour depended solely on a new genetic mutation, then it would typically take many generations before this new niche constructing behaviour could spread through a human population by natural selection and genetic inheritance, and therefore a proportionally long time before it could modify a natural selection pressure in an environment. However, if a new niche-constructing behaviour depended instead on a cultural innovation, such as the invention of a new artefact or of a new agricultural technique, then this niche-constructing behaviour might spread through the same human population very rapidly, possibly even within a single generation, as a consequence of its cultural diffusion (Cavalli-Sforza & Feldman, 1981; Rogers, 1995). Thus human cultural niche construction may sometimes modify a natural selection pressure in an environment, or create a culturally generated ecological inheritance, much more quickly, and possibly far more radically, than could any kind of non-cultural human niche-constructing activity. So it may be possible for human culture to impose unusually intense selection pressures on human genetic evolution, as well as on the genetic evolution of other species that happen to be affected by the same human niche constructing activity.

3.1. Beyond Sociobiology

The inclusion of niche construction in evolutionary theory is likely to change our understanding of the relationship between human genetic evolution and human culture.

First, it creates difficulties for a celebrated earlier attempt to integrate human culture and human genetic evolution, namely human sociobiology. Sociobiology is firmly based on standard evolutionary genetic theory

(Wilson, 1975). This is portrayed in Figure 3a (note the similarities between Figure 3a and Figure 1). Classical sociobiology (Wilson, 1975) assumes that genetic inheritance is the only inheritance system in biological evolution. Transmitted genes influence the ability of individual humans to survive and reproduce differentially (relative to exclusively independent sources of natural selection in their environments) and to pass on their genes to their descendents via genetic inheritance. When cultural inheritance is recognised (Lumsden & Wilson, 1981; Dawkins, 1989), it is generally assumed to influence the adaptation of humans relative to their selective environments, rather than to modify natural selection pressures in their selective environments. For sociobiology, human phenotypes, including human cultural phenotypes, possess the same status in evolution as do the phenotypes of every other species. They are just "vehicles" for their genes (Dawkins, 1989).

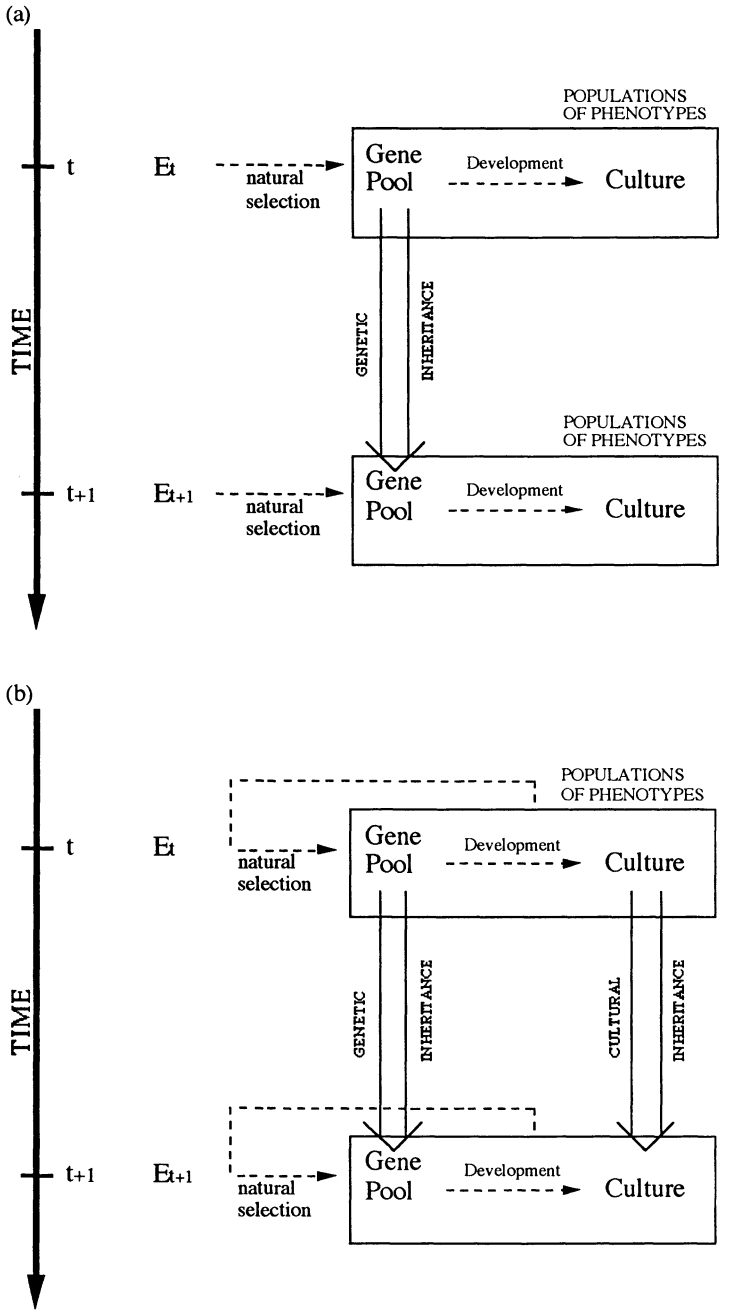
If the theory of niche construction is correct, however, this sociobiological perspective cannot be sufficient because it ignores both the additional niche-constructing role of phenotypes in evolution, and the contribution of culture to this added role. Phenotypes, including cultural human phenotypes, survive and reproduce differentially relative to natural selection pressures in their environments, and they modify some natural selection pressures in those same environments by niche construction. Phenotypes may thus generate an ecological inheritance in addition to genetic inheritance (Figure 2), and may thereby introduce a second general inheritance system to biological evolution, one to which, in the human case, human culture can directly contribute (Feldman & Cavalli-Sforza, 1976).

Sociobiology was later challenged by gene-culture coevolutionary theory (Feldman & Cavalli-Sforza, 1976; Cavalli-Sforza & Feldman, 1981, 1983; Boyd & Richerson, 1985, 1995; Durham, 1991), which, with some variations, proposed a scheme along the lines summarised in Figure 3b. These theorists emphasised that human culture is based on its own separate cultural inheritance system, but unlike the sociobiologists they noted that human culture, under the influence of cultural inheritance, does sometimes modify natural selection pressures in human environments (Feldman & Cavalli-Sforza, 1976; Feldman & Laland, 1996; Laland, Kumm, & Feldman, 1995).

The conceptual model in Figure 3b is clearly an advance on sociobiology's view, but it still oversimplifies the relationship between genetic

Figure 3a. Standard evolutionary theory as the basis of sociobiology. Culture affects the differential survival and reproduction of phenotypes relative to natural selection, but culture does not contribute to human biological evolution in any other way.

Figure 3b. Gene-culture coevolutionary theory based on standard evolutionary theory, and without niche construction. This theory introduces cultural inheritance, and some evolutionary feedback generated by human culture, for example by agriculture.


(a)
TIME
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evolution and human culture in two respects. One is that the proponents of gene-culture co-evolution originally tended to regard the capacity of phenotypes to modify natural selection pressures in their environments as an exclusively human capacity. However, niche construction is a very general phenomenon. The phenotypes of most, if not all, species niche construct to some degree (Lewontin, 1983; Jones, Lawton, & Shachak, 1997). Therefore niche construction cannot depend exclusively on culture. The second is that in the absence of niche construction and the ecological inheritance system that it gives rise to, gene-culture coevolutionary theory addresses how human cultural inheritance interacts with human genetic inheritance, but it does not include the effect of culture on the external environment, for example, on abiotic features.

In an attempt to overcome these two problems, we propose an extension of these earlier gene-culture co-evolutionary models that takes the two further steps illustrated in Figure 4. By expanding the box labeled "populations of phenotypes" in Figure 3b, Figure 4a makes the point that human niche construction is not just a cultural process. It shows that human niche construction potentially involves multiple processes at three different levels. Two of these levels, the genetic level and the ontogenetic level, are implicated in the niche-constructing activities of many species, but the third, cultural level is close to being exclusively human (Odling-Smee, 1994, 1996). To give a simple example of plural-level niche construction in humans, the aggregation of our ancestors into large-scale communities must have involved a lot of cultural niche construction (Sherratt, 1997). However, one probable consequence of this human aggregation, the production of large amounts of raw sewage in small areas, is clearly not cultural. It is something most animals produce when they aggregate in small areas, and they do it for physiological not cultural reasons. As such, the accumulation of raw sewage is a population-level, rather than a cultural-level form of negative niche construction. It is a health hazard, and therefore a likely source of one or more modified natural selection pressures in village or urban communities.

The second step, which is illustrated in Figure 4b, then adds ecological inheritance to the other two human inheritance systems, leaving us with three different inheritance systems to contend with in human evolution. They are: (i) standard evolutionary theory's genetic inheritance which is directed by natural selection; (ii) ecological inheritance, comprising legacies of modified natural selection pressures, directed by niche construction; and (iii) cultural inheritance, comprising culturally acquired knowledge, directed by various developmental and cultural selection processes (Boyd & Richerson, 1985, 1995; Durham, 1991; Soltis, Boyd, & Richerson, 1995). Unlike both genetic inheritance and ecological inheritance, cultural inheritance is not a general inheritance system in evolution but, if we leave aside

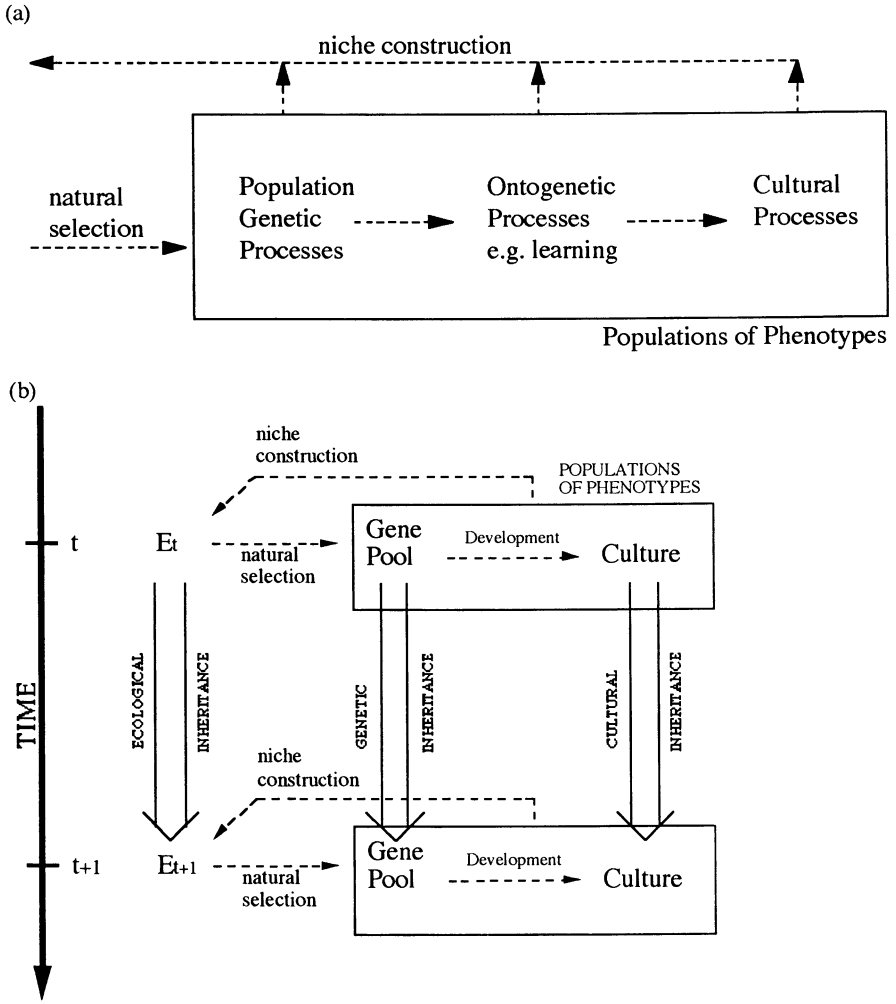

Figure 4a. This figure expands the boxes labelled "populations of phenotypes" in Figure 3b. Adaptation in populations of complex organisms, such as humans, depends on population genetic processes, knowledge-gaining ontogenetic processes, and cultural processes, all of which can generate niche construction.

Figure 4b. The extended gene-culture coevolutionary framework based on three human inheritance systems. Cultural inheritance affects human genetic inheritance by affecting the differential survival and reproduction of diverse individual human beings. Cultural inheritance also affects human ecological inheritance by contributing to human cultural niche construction.

transient animal proto-cultures, it is almost uniquely human (Boyd & Richerson, 1996). However, by contributing to both of the roles of phenotypes in evolution, their survival and reproduction role, and their niche-constructing role, human cultural inheritance can influence both the other two general inheritance systems in human evolution. We are therefore proposing the triple inheritance scheme shown in Figure 4b, and we suggest that this scheme provides us with the basis of a more complete picture of human gene-culture coevolution.

3.2. The Human Past, and the Human Future

To what extent are the human sciences likely to be affected by this extended picture of gene-culture coevolution (Figure 4b)? We will not attempt to work through specific topics in detail here (see Laland, Odling-Smee, & Feldman, in press). Instead we will end by discussing two large-scale issues in broad terms, as a way of suggesting the kinds of difference our approach may make. One issue refers to the human past, the other to the human present and future.

First, substituting the framework of niche construction (Figure 4b) for that of standard sociobiology (Figure 3a) could change our understanding of past hominid evolution quite significantly. If our framework is correct, hominid evolution cannot have been directed solely by independent sources of natural selection, as standard evolutionary theory currently maintains, but instead it must have been co-directed by cycles of natural selection and hominid niche construction. For example, any new episode in hominid evolution could equally well have been orchestrated by either natural selection or niche construction.

Second, regardless of whether a new episode in evolution is mediated by natural selection or by niche construction, it is likely to promote a feedback cycle between natural selection and niche construction. One example of human niche construction that modified the natural selection of some other human trait is suggested by Aiello's and Wheeler's (1995) expensive tissue hypothesis concerning the evolution of the human brain. The human brain is an expensive organ, yet there is no elevated basal metabolic rate in humans to pay for our enlarged brains. This led Aiello and Wheeler to search for a human organ that suffers a shortfall of resources to pay for the brain. This organ is the gut, but how could our ancestors have afforded a reduction in gut size without a loss of fitness?

Aiello and Wheeler proposed that our ancestors must have used their brains to improve their diets in proportion to their loss of gut. They suggested that this happened in two episodes, the first episode coinciding with the appearance of the genus *Homo*, approximately two million years ago,

and supported by increased meat eating, the second coinciding with the appearance of archaic *Homo sapiens* during the latter half of the Middle Pleistocene, and supported by the cultural invention of cooking, and hence by the externalisation of part of the digestive processes. Aiello and Wheeler stress that their hypothesis does not imply that the evolution of the human brain was actually caused by these brain-invented dietary changes, but that it was permitted by it.

Their hypothesis is plausible and based on some hard initial facts. Of central interest here is that Aiello's and Wheeler's hypothesis exemplifies how the niche-constructing activities of a population can feed back to affect its own subsequent genetic evolution, by modifying one of its own natural selection pressures. In this case an expensive large brain furnished our ancestors with the complex information-processing capacity they utilized in hunting, tending fires, sharing food, and cooking. The same brain may then have offset its own fitness costs by allowing metabolic savings at the level of the gut through the modification of natural selection pressures in hominid environments, first through increased meat eating (which may have depended on culture) and then by cooking (which must have depended on culture). Thus the human brain probably permitted the further evolution of itself.

Turning towards the future, our scheme of human gene-culture coevolution (Figure 4b) may also have relevance to both contemporary and future human life. Superficially, this may seem unlikely because we are a long lived species with a slow generational turnover, which ensures that the rate of human genetic evolution is generally slow. It might therefore take millenia for any change in our selective environments induced by contemporary cultural niche construction to change our genetics. Conversely, the rate at which we are currently introducing changes in our environments through our cultural activities is fast, and is getting faster. Therefore, we might alter our environments many times over by cultural niche construction, long before any coherent genetic response could occur in a human population. In these circumstances it could easily be argued that the effects of contemporary human cultural niche construction on human genetic evolution are likely to be irrelevant to contemporary human affairs, and may be ignored in practice.

This objection is probably misleading, however, for two reasons. First, culturally induced genetic evolution in humans is not necessarily slow. For example, Kumm, Laland, and Feldman (1994) explored some of the interactions between human genetic and cultural processes in human infanticide. They looked at how a culturally transmitted cultural trait, a bias in favour of killing human infants of one sex only, usually females, affected the natural selection of a distorter gene that was assumed to influence both the primary and the adult sex ratios in the same human population. If the initial frequency of this gene in a population was close to zero, then it could

indeed take many hundreds of generations before anything significant happened at the population-genetic level in response to the culturally modified natural selection. However, if the initial frequency of the same gene was at some intermediate level in the population (which is not implausible), and if the natural selection generated by the cultural trait was strong (and natural selection can be very strong when imposed by culture), then a significant genetic change could occur in a human population in response to its own cultural niche construction, surprisingly rapidly. Similarly, in their study Laland, Kumm, and Feldman (1995) reported that detectable genetic changes emerged after as few as two or three generations. In some circumstances, culturally induced genetic evolution can be fast.

A second reason for not ignoring the interactions between contemporary human culture and human population genetics is precisely that human genetic evolution is generally slow, whereas the human modification of human environments can be quite fast. Thus contemporary humans risk generating changes in modern human environments through cultural niche construction, and therefore changes in human natural selection pressures, at a faster rate than human genetic evolution can track. The different rates at which human genetic processes and human cultural processes operate might raise some new problems for human adaptation.

One simple way to illustrate the logic behind this idea is to choose a fanciful, yet topical, example of human technological niche construction, say the production of CFC gases, and to consider its possible gene-culture coevolutionary consequences. Assuming that the environmental consequence of the production of CFCs is a hole in the ozone layer, could this particular case of negative cultural niche construction affect human genetic evolution through a self-induced, culturally modified natural selection pressure consisting in increasing ultra-violet light?

Probably not, because we are likely to adapt to the possibility of increasing ultra-violet light exclusively at the cultural level, by canceling out any threat of a self-induced natural selection pressure through further positive cultural niche construction, thereby protecting our genetics from further natural selection. Appropriate cultural adaptations could take several forms: anything from wearing protective clothing to using better sun creams, to changing our industrial practices until the hole in ozone layer disappears. Provided the cultural response is adaptive, and provided it acts rapidly enough, then we might have nothing worse to fear than a culturally imposed "problem" that is "solvable" by a culturally imposed "solution." Referring back to an equivalent example from the past, if the Kwa-speakers had possessed the appropriate technology (for instance to kill mosquitoes or to nullify malaria), they could have protected themselves, by cultural means, from the intensified natural selection by malaria that resulted from their own agricultural niche construction.

However, should we fail to adapt sufficiently to any culturally imposed problem with a culturally imposed solution, then feedback could occur from negative human cultural niche construction to human population genetics, in the form of a culturally modified natural selection pressure selecting for different human genes. Presumably, this is what did happen to the Kwa-speakers in the past, and it could happen again, in other human populations in the future, possibly even in the case of the CFC gases. If it did, then a modified natural selection pressure, associated with a culturally generated ecological inheritance, would cause additional differential deaths among human beings, either directly (increasing ultra-violet light coming through a hole in the ozone layer might kill those individuals who carry genes predisposing them to cancers), or indirectly instead (ultra-violet light might destroy a vital human food resource, for example).

In sum, our gene-culture coevolutionary scheme (Figure 4b) allows the rapid rate at which we can set ourselves new adaptive problems by cultural niche construction to occasionally exceed the relatively slow rate at which these same novel adaptive problems could be "solved" by further human genetic evolution under modified natural selection pressures. Moreover, this particular possibility may be human specific. Many other species have probably contributed to their own extinction in the past as a consequence of their own negative niche construction. However, no species other than our own possesses a cultural inheritance system of sufficient cumulative power to modify its own natural selection so quickly, or so radically, through cultural niche construction (Boyd & Richerson, 1996). Therefore, should we humans ever drive ourselves to extinction, we will probably do so as a consequence of negative cultural niche construction.

Understanding this point in terms of the extended gene-culture coevolutionary theory illustrated in Figure 4b may therefore be relevant to contemporary human socio-cultural affairs. To be sanguine, it could even contribute to the maintenance of human adaptation in a rapidly changing world.

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Chapter 5

BIOLOGICAL AND MATERIAL CULTURAL EVOLUTION: ARE THERE ANY TRUE PARALLELS?

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ABSTRACT

"Evolution" in both biological and material cultural domains entails stability and modification of transmissible information. "Descent with modification" in both domains automatically generates hierarchically structured sets of genetic and material cultural information, respectively. With rare exceptions, evolutionary biological systems are arrayed in a single hierarchical system (as delineated, for example, in the Linnaean hierarchy). On the other hand, because of a different mode of inheritance entailing lateral transmission of information ("theft of idea"), the products (historical patterns) of material cultural evolutionary history are typically represented in more than one hierarchical structure, all of equal validity.

Though selection, natural and cultural, is a real mechanism underlying stasis and change in both domains, naïve selectionism (the assumption that evolutionary history is simply the result of selection extrapolated over time) is insufficient to explain actual repeated historical evolutionary patterns in either domain. Rather, evolution is the fate of heritable information in an economic context. Recent work in biological evolutionary theory has shown that the intersection of economic (that is, ecological) phenomena with genetic systems takes place at a spectrum of spatiotemporal scales.

Perspectives in Ethology, Volume 13: Evolution, Culture, and Behavior
edited by Tonneau and Thompson, Kluwer Academic/Plenum Publishers, New York, 2000

Similarly, material cultural evolution stems from the interplay between information and economic systems organized at various spatiotemporal scales.

Though detailed biological examples of phylogenies and patterns of extinction and radiation are well documented in the literature, well-analyzed examples of material cultural evolution are comparatively rare. I present such an analysis of the design history ("evolution") of nineteenth- and twentieth-century cornets in part to rectify this lack of well-analyzed examples, and to stress that the validity of evolutionary theory ultimately rests on how well it explains repeated patterns in the history of life or of material cultural systems.

1. INTRODUCTION

Ever since Herbert Spencer (1863), following closely on Darwin's heels, began to write about human social and cultural evolution (see Carneiro, 1973), parallels have been sought between biological and cultural evolutionary domains. In an earlier paper (Eldredge, 1997), I pointed out that the relevance of biological evolutionary models to economic theory depends very much on the particular form of biological evolutionary theory chosen—there being manifestly more than one version of biological evolutionary theory available today. The present essay extends this theme to *material cultural evolution*—how artifacts and implements, for example, change over time. I argue that biological evolutionary theory, because its competing versions are often more developed and well grounded in empirical patterns emanating from the laboratory, the field and the fossil record, has much to offer to the theorist tackling material cultural evolution. I also try to formulate an evolutionary model of the interaction among hierarchically structured systems of material cultural information and economic systems—a model that is not limited purely to analogies between natural and cultural selection (contrast Boyd & Richerson, 1985).

Although my main intent is to suggest a meta-theoretical, structural framework for a general theory of material cultural evolution, the actual content of that theory must of course derive from a serious contemplation of actual patterns in material cultural "evolutionary history." As in biology, it must be the raw data and their first-order interpretations that yield repetitive historical patterns (Eldredge, 1999) suggesting the content, and affording the tests of, any overarching theory of evolution. We will ultimately derive a more complete and satisfactory evolutionary theory from such historical patterns, integrated with knowledge of dynamic processes such as natural or cultural selection.

As far as material cultural information is concerned, however, only a few detailed case histories of design "evolution" have been worked out. This essay includes an outline sketch of cornet (soprano valved brasswind musical instrument) history from roughly 1850 onward, and presents an overview of cornet "morphological" (design style) diversity that highlights its early phases of development. I am particularly interested in tracing the evolution of design of what has come down to us as the "modern" cornet.[1] A basic introduction to the definition and anatomy of cornets can be found in the caption of Figure 1, which depicts the Besson "Concertiste," and in the following illustrations.[2] No detailed history of the cornet is available yet, nor have extensive monographs on the history of the more important cornet makers been published; however, some are in preparation.[3]

2. THE INFORMATIONAL BASIS OF BIOLOGICAL AND CULTURAL EVOLUTION

Dawkins (1976), in the eponymous book in which he coined the expression "selfish gene," also suggested "memes" as the cultural evolutionary counterpart to "genes." The particulate and, especially, corporeal, nature of genes was first glimpsed through Mendel's early experiments, and subsequently came clearer through the efforts of a number of gifted researchers in the first decade of the twentieth century, especially in Thomas Hunt Morgan's laboratory at Columbia University; finally, the physical structure of genes was worked out in minute base-pair detail during the molecular revolution that began in the 1950s and still goes on.

[1] That is, excluding "cornets" with other than perinet valves, or with bells to the right of the valve assembly ("modèle français"), as defined in passing below.

[2] The Besson Concertiste, redesigned in 1888 from its original early 1870s version, is the standard design configuration for almost all post-1920s cornets—albeit in "long-bell" (i.e. non shepherd's crook) form, and with a fixed leadpipe to receive the mouthpiece (see Figure 1, caption for definition of terms). The Concertiste was also widely copied in its earliest days. A partial list of makers who emulated the original shepherd's crook Besson Concertiste with removable leadpipe shank includes: Association Générale des Ouvriers Réunis, Bohland and Fuchs, Boosey & Co., Couesnon, Distin, ?Gautrot, Higham, J. W. Pepper, Salvation Army, J. Thibouville-Lamy, Thompson and Odell, J. Wallis & Son. A host of "stencil horns," many made by eastern European manufacturers, also emulated the Concertiste. A partial list of modern era makers who have produced the Besson Concertiste in its modernized, long-bell form, includes: Bach, Blessing, Boosey and Hawkes, Buescher, Conn, Holton, Frank, King, Martin, Monette, Muck, Olds, Taylor, York.

[3] For example, my working manuscripts on the Besson company of both Paris and London (Eldredge, unpublished ms. A) and the Courtois Co. (Eldredge, unpublished ms. B), and M. D. Banks's forthcoming study of the Conn Co.

No such empirical demonstration of memes has been forthcoming. Yet Williams (1992) is surely right when he distinguishes between genes as corporeal entities and the particulate pieces of information that each gene carries. And even if attempts to speak of memes purely as small, perhaps "segregating," indivisible elements of (material) cultural information in the end proves fruitless, thinking in terms of "memetic information" certainly makes sense. For cultural ideas are clearly transmissible, though in ways different from genetic information. The major difference between the physiological process of genetic inheritance and the learned acquisition of cultural information is nicely captured by the term "memetic" itself: transmission of material cultural information comes when humans are literally taught how to make something, or simply copy what they see—or a mixture of both.

2.1. Implications for Evolutionary Rates

This great difference in mode of inheritance may have profound evolutionary consequences. Much has been made of the potentially much faster rate of change that the "lateral" transmission of material cultural information can offer, as compared to the severe constraints on the passing on of one half of each parent's genes in sexual reproduction. Indeed, much has been made of the acceleration of technological change since the Industrial Revolution (or even since the Paleolithic: see Eldredge & Tattersall, 1982). The mode of transmission of material cultural information undoubtedly facilitates such rapid rates. However, the potential for rapid modification of material cultural information afforded by its mode of transmission should not be taken as itself constituting a *cause* of rapid change.

Consider the exact parallel in biological evolution: Simpson (1944) discussed the null hypothesis that organisms with shorter generation times, having more opportunity to accumulate mutations, and undergoing more intense natural selection (i.e., differential reproductive success) than organisms with longer generation times, should on the average evolve more rapidly. He then demolished the notion by comparing rates of mouse and elephant evolution: Though arguably more speciose, mice have remained anatomically and behaviorally much more conservative than elephants, considering the great array of sizes, shapes, and in particular, dental adaptations that have marked the latter's evolutionary history. Simpson's example graphically illustrates that mode of inheritance is not itself a direct cause of evolutionary rates. Similarly, Darwin (1859) was able to establish the principle of natural selection while relying on a completely incorrect theory of genetic transmission—a fact which further underscores the decoupling of what Dobzhansky (1937) called "physiological genetics" from the fate of genes in a population of individuals ("population genetics").

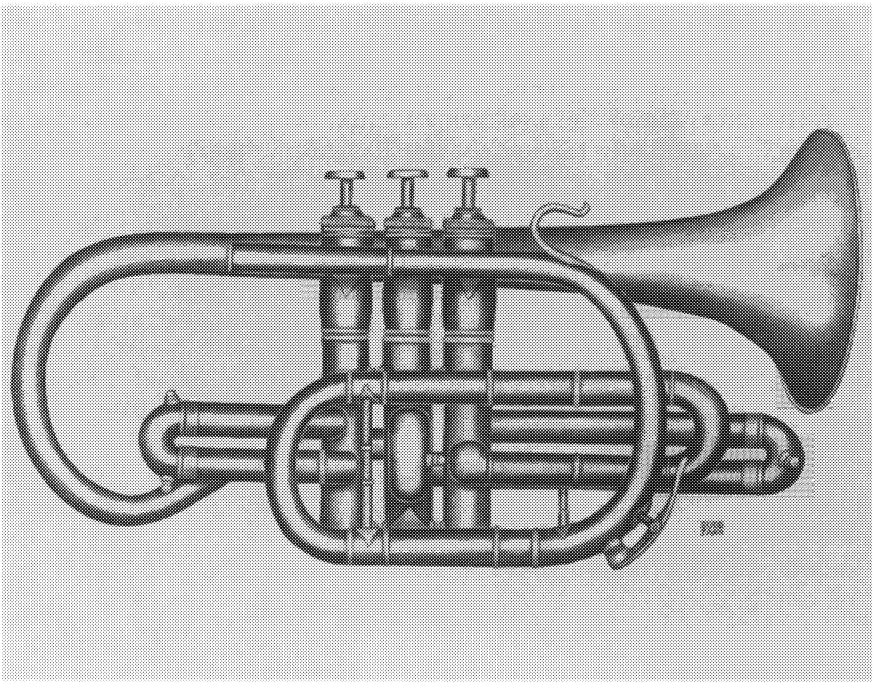


Figure 1. The quintessential cornet—the Besson "Concertiste"—designed by the F. Besson company in Paris in the early 1870s, and redesigned in 1888 to the model shown here. This model is the forerunner of most modern cornets. Profile view of right side of the instrument, showing leadpipe (without the mouthpiece-receiving removable shank), which runs forward, curving deeply down to water key, running backwards, reflecting up into a tuning crook (or "slide"), then running forward, reflecting downward in a second tuning slide (removable for "high" and "low" pitch), finally joining the third valve. The leadpipe has a total of one turn and a half (typical of most 19th-century cornets, regardless of model) and markedly differs from that of the longer Bb trumpet, which has only a single 180° turn (the tuning slide facing forward). Also shown are the three perinet valves, each associated with a tunable crook. Depressing the valves adds the length of the tubing associated with each valve to the total length of the instrument. The "bell" exits the rear of the first valve, is bent into a "shepherd's crook" configuration, and runs forward to the bell flare. The configuration of the leadpipe, with its two tuning slides all situated (from this perspective) outside the third valve slide, is the *sine qua non* of the Concertiste model. Cheaper imitations of the previous century did not have a movable second slide on the leadpipe; with the exception of very recent horns of the "revival" period, post-1920s versions also lack a movable second leadpipe slide, have "fixed" leadpipes (non-removable shanks) to receive the mouthpiece, and longer bells with no shepherd's crooks. Note the relationship of the valve slides (plus the leadpipe and bell connections to the valves) with the two connecting pipes between the valves: This format is seen in virtually all cornets and trumpets in production today. Total length: 13″. Drawing by Budd Jahn (also Figures 2, 3A, 3B, 4, and 7) based on F. Besson (Paris) serial no. 72036 (ca. 1907) in the author's collection.

A similar point applies to material cultural evolution: The capacity for rapid change afforded by instruction and copying implies that no "generations" can be discerned, and that all who are exposed to the relevant information (not a limited subset of "offspring") may potentially make use of it. However, we should not expect design to be in constant flux. Indeed many examples of great conservatism or "stasis" permeate design history. From the early 1870s to the late 1930s, for example, the "Desideratum" style cornet (Figure 2) was produced by the Besson company and many of its imitators with only slight changes to the original design (substitution of a "fixed leadpipe").[4] The model persisted in Besson hands with only minor variations, and astonishing faithfulness in terms of certain details.

Patterns of evolution in the material cultural domain, just as in the biological evolutionary realm, are thus decoupled from, rather than a direct reflection of, the mode of transmission of the underlying information. Comparing rates of change across the two realms (not, in any case, a wholly realistic enterprise: how does one truly compare rates of change in cornets and elephants?), one might nevertheless expect cultural evolution to proceed much more quickly than evolution in all biological systems save, perhaps, viruses and bacteria.

2.2. Implications for Evolutionary Trees

An equally striking consequence of the difference in mode of transmission of biological and cultural information is the geometry of the resulting evolutionary trees. Darwin (1859; see Eldredge, 1999, p. 80ff.) used the Linnaean hierarchy—and his sole illustration, a sketch of a series of phylogenetic trees, published as an interleaf between pages 116 and 117 of the first edition of the *Origin*—as his main pattern to argue that evolution happened. Darwin argued that if evolution (his "descent with modification") occurred, then we should expect to see a hierarchically nested set of relationships among taxa in the living world and the fossil record. And that is precisely what Linnaeus, of course, more than anyone else before him, had already demonstrated: the structure of life, based on patterns of resemblances, in fact truly is hierarchical. Working it the other way round, Darwin argued that

[4] Early cornets had removable "shanks" connecting the mouthpiece to the instrument; differently sized shanks yielded different pitches to the instrument, viz. C, Bb (most common), A and Ab. Fixed leadpipes, on the other hand, are permanent parts of the horn in which the mouthpiece is inserted; in this case, change of pitch was effected by systems of rotary valves or moveable slides (ultimately dispensed with altogether). See discussion below; also Figure 1 and discussion in Footnote 8, of the "Fin de Siècle" model.

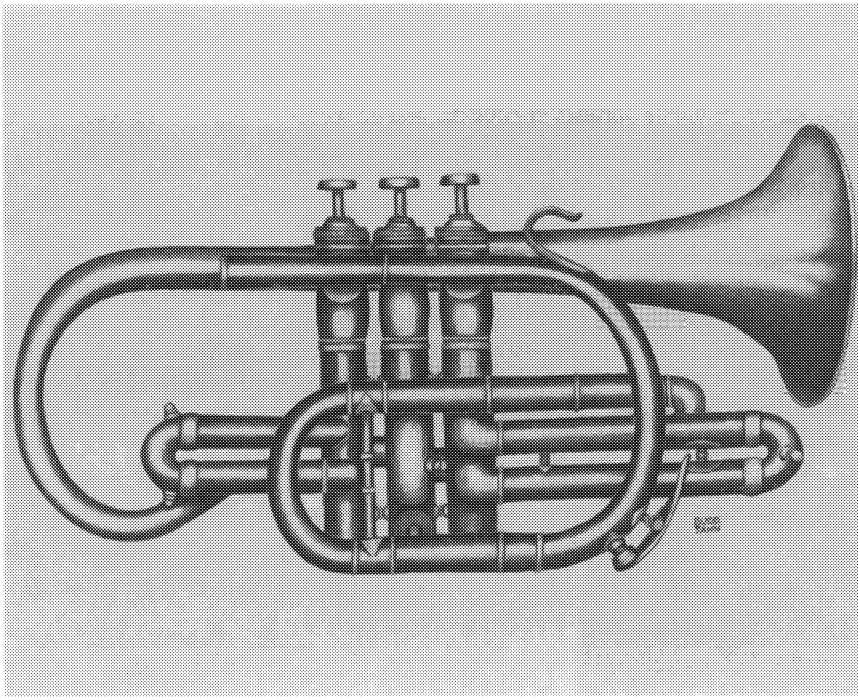


Figure 2. The Besson Desideratum model. The main difference in configuration between the Desideratum and the Concertiste models is the relationship of the leadpipe to the third valve slide. In the Desideratum, the upper and lower tubes of the third valve slide emerge to the right of the third valve (towards the viewer in this perspective), and then are reflected forward. Therefore, the last portion of the leadpipe (bearing the second, smaller, high/low pitch tuning crook) is located to the *left* of the third valve slide. There were many relatively minor (though consistent for many years) differences in bracings and ferrules between the Concertiste, a lighter and brighter-sounding instrument, and the Desideratum. Whereas the Concertiste was Besson's most expensive model, at least from the 1890s to the advent of World War I, the Desideratum was their second most expensive. Although the relationship of the intervalve portings to the placement of valve slides, and bell and leadpipe articulation to the valves, is geometrically identical in both the Desideratum and the Concertiste, the bowed-out shape of the Concertiste intervalve portings ("perce pleine") is the design heavily favored in today's trumpets and cornets. Total length: 13″. Drawing based on F. Besson (Paris) cornet, serial no. 78092 (ca. 1911) in the author's collection.

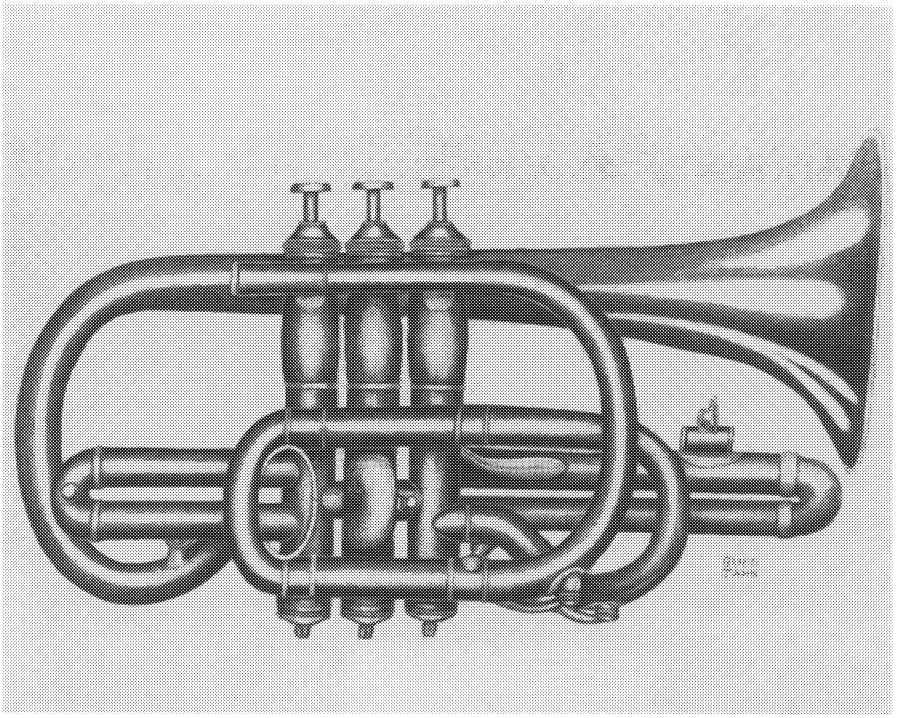
once lineages diverge (and they must have diverged, as there is more than one species of living things on the planet), what happens to them in terms of further modification will not affect ("show up" in) collateral lineages; only descendants will inherit evolutionary novelties, in the same or further modified form. Looking from the top down, the tips of the nearest branches of the evolutionary tree are those species most closely related to one another; the further away the branches, the less resemblance among them. But surely

some resemblances must remain linking up all forms of life, *if* all life has actually descended from a single common ancestor.

No such neat pattern can be expected in material cultural evolution. Despite repeated attempts I have repeatededly failed to produce even a simple dichotomous key, or rudimentary classification, of cornet models. Certainly there are distinguishable models, very often running "true to type" for many years, and always remaining quite distinguishable from other models. Consider, for example, the aforementioned "Desideratum" style (Figure 2). The major feature of this model is that the third valve slide extends laterally to the right of the horn as it is held by the player, and then runs straight forward.[5] A major rival—indeed probably the most prestigious model of cornet in use from the 1860s through 1900—was invented by the Courtois company (also Parisian) in the mid-1850s (see Figures 3A, 3B). This classic Courtois design had a characteristic "droop" to the leadpipe just before it entered the third valve, enabling the two water keys, operated by a single lever, to be in the same horizontal plane or nearly so. In the Besson Desideratum (Figure 2), the last curve of the leadpipe was a tunable slide (for pitch changes). It always consisted in a simple curve, and never formed into a droop. The Courtois, on the other hand (Figure 3), always included a droop, and never a removable slide. The difference seems to have been indelibly fixed, as both models were widely copied by many makers in Europe and North America.[6]

[5] Valved instruments have tubing associated with each valve, changing the overall length of the instrument when the valves are depressed (singly or in combination). Valves were the last of a series of inventions enabling brasswind instruments to play a full (twelve-tone) chromatic scale in all registers; see Baines (1976, 1992) for details on brasswinds generally, and on the various systems of holes, keys, slides and valves that have been fitted to brasswinds since the Renaissance. The configuration of the third valve slide in the Desideratum model (Figure 2) constitutes an "adaptation," the thought goes, to avoid hitting the bell as the slide is removed in the common circumstance of minor damage to slide alignment; the rival "Concertiste" design (Figure 1), for example, has a very narrow tolerance between the third valve slide and the bell flare. In many older horns the slide cannot be removed because of the changed position of the bell.

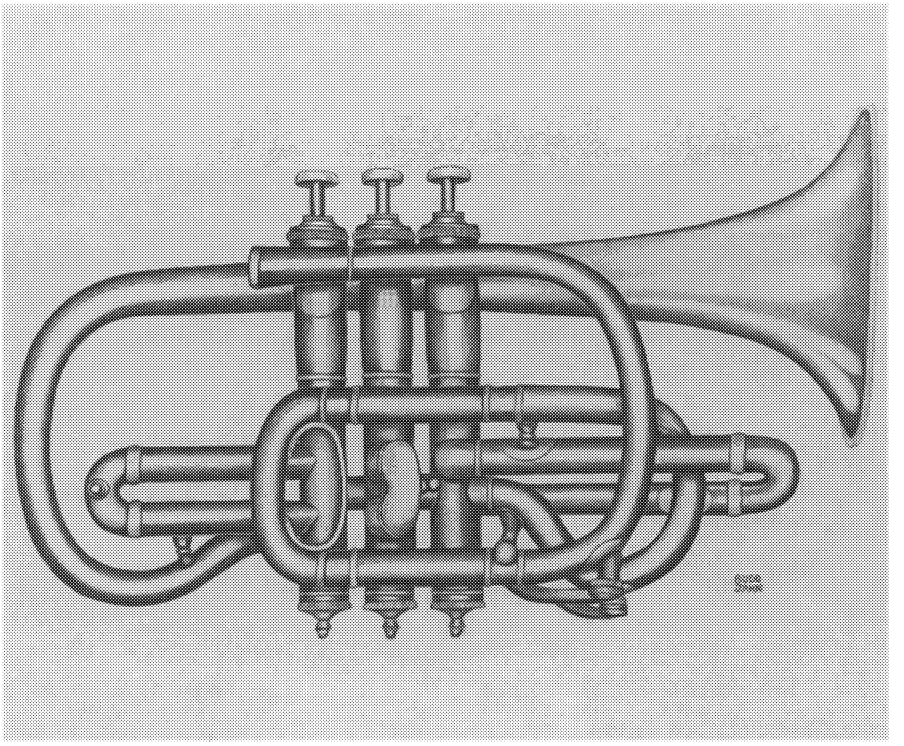
[6] A partial list of companies other than French and English Besson that produced, at various times, Desideratum-style cornets (with removable shanks or fixed leadpipes; with or without short "shepherd's crook" bells), includes: Carl Fischer (Austrian import), Courtois, Distin (and later Keefer), Frederick, Hawkes and Son, J. W. Pepper, Kaempf, Kalashen (dealer), Missenharter, Pélisson-Guinot-Blanchon, Standard Band Instrument Co. (and later Vega). The list of Courtois copies is even more extensive. The following partial list makes no distinction between the two subtypes of Figures 3A and 3B; nor does it include Conn or the Boston Musical Instrument Manufactory, some of whose horns were at the very least inspired by the Courtois designs: Association Générale des Ouvriers Réunis, Bohland and Fuchs, Boosey and Co., W. Brown and Sons, Busch, Coeuille (though Conn-like), Couesnon, DeLacy, Distin (England; U.S.), Gautrot, Higham, Hileron (stamp name—?Gautrot), J. W. Pepper, Lehnert, Leland, Lyon and Healy, Metzler (possibly Gautrot), Pollmann, Slater, Standard Band Instrument Co., York (Conn-Wonder-like).



A

Figure 3. The two classic Courtois (Paris) models. Both models have a double waterkey, operated by a single lever, in nearly the same plane, achieved by a characteristic downward droop to the last (and non-movable) crook of the leadpipe. The droop and characteristic nipples on the bottom valve caps give these two Courtois designs (and their many imitations) the look and feel of the quintessential late nineteenth-century cornet. Figure 3A: Entire leadpipe assembly to the right of the third valve slide; variously stamped or advertised as Koenig, then Levy's (small bore), Arbuckle (medium bore), and Emerson (large bore); all four were virtuoso players. Total length: 12 1/2″. Based on Courtois serial no. 15548 ("Arbuckle"), ca. 1880, in the author's collection.

Manufacturers also blended styles, copying the successful models, to be sure, but sometimes producing what seem to be "hybrids" between major designs. For example, an advertising poster published ca. 1885 (see Banks, 1994, cover illustration) shows a model of the great cornet inventor and musical instrument manufacturer Charles Gerard Conn: a Desideratum-style cornet (Figure 2) with a drooping curve and a double water key (as in Figure 3)! To my knowledge, no one currently owns such an instrument, even though collections of Conn's horns are



B

Figure 3B: Final portion of leadpipe passes between upper and lower branches of the third valve slide, which is inclined downwards and to the right. Arban model (though never stamped as such, and only known through advertising; Arban was perhaps the first cornet virtuoso). I have noted one instrument in this configuration stamped Levy's model, 1870. Total length: 12 1/2″. Drawing based on Courtois serial no. 19108 (ca. 1890) in the author's collection.

extensive.[7] Such horns, though rare and obviously never in extensive production, nonetheless demonstrate that virtually anything is possible in terms of mixing-and-matching elements of cornet design; which raises the possibility that "memes" as segregating portions of information may have some use in the material cultural domain.

What happens to a cornet design lineage after it appears as distinct from other designs may thus "affect" (be incorporated into) the manufacture of those other designs. This is as true of the patterns of subsequent

[7] Another example of "hybrid" was recently auctioned on the internet EBAY—a "Henri Farny" (about whom or which nothing is known); the horn was a Desideratum with a droop, but nonetheless with a single water key.

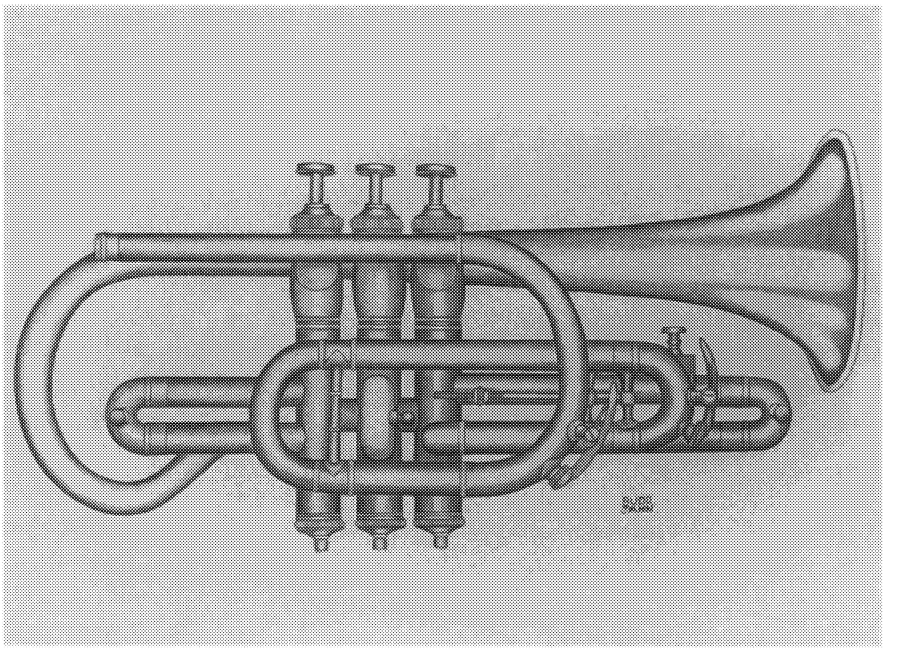


Figure 4. Fixed-leadpipe version of the "Fin de Siècle" model. This model is an adaptation of the original Besson Concertiste design (Figure 1). Notice the substitution of a permanent longer ("fixed") segment of the leadpipe, replacing the removable-shank system rendered obsolete by the conversion of the second (high/low pitch) tuning slide to a slide regulated by a stop rod. A "quick pull" on the slide brought it into position for "instantaneous" change of pitch from Bb to A. Total length: 14″. Drawing based on Jérôme Thibouville-Lamy (Paris) instrument, ca. 1905.

modification of successful cornet design lineages as it is of the rare hybrids. Consider, for example, the "Fin de Siècle" ("end of the 19th century") model (Figure 4). I take the model name from a catalogue of the Association Générale des Ouvriers Réunis. Made by many manufacturers,[8] the "Fin de Siècle" was the first commonly produced cornet model with a fixed leadpipe

[8] Yet another Parisian company, the Association Générale was formed in 1865 when a number of skilled brass instrument craftsmen, apparently fed up with long hours and low wages, created their own manufacturing business—wisely hiring veteran brass manufacturing entrepreneurs (initially F. Neudin and François Sudre) to oversee their operations (Waterhouse, 1993, p. 11). The "Fin de Siècle" appeared in the mid-1890s, and still had a detachable shank—as did a similar Conn model of the same period allegedly called the "Concert Model" (the design, with a slide and a stop rod to allow a quick adjustment from C-to-Bb-to-A, being a modification of the Besson "Concertiste"). Modifying the second slide of the leadpipe of Concertiste-style cornets to assume the function of actual key change made the removable leadpipe redundant. Manufacturers thus quickly switched to a single, "fixed" leadpipe—

and a slide with a stop-rod (usually, though not invariably, in the center), which allowed a "Quick Change" to the key of A from Bb. These instruments were in essence modifications of the Besson Concertiste (Figure 1) with the substitution of a fixed leadpipe for the removable shanks.

If, as seems probable, this new design was the first commonly made fixed leadpipe Bb-A cornet, it was followed, or paralleled in time, or perhaps even preceded (the data are insufficient to decide) by a similar addition of a fixed leadpipe to the Besson Desideratum (as, for example, by the Standard Band Instrument Company of Boston), replacing the high/low pitch second slide on the leadpipe. In other words, the fixed leadpipe/stop-rod-controlled quick-change slide was effectively applied, not only to the Besson Concertiste, but also to any other cornet that had a second interchangeable slide used for high and low pitch.

Thus, unlike a biological evolutionary novelty confined to a single lineage (such as tusks in elephants), novel ideas can be applied to more than one design—and not just by the innovating company, but often independently by others. Admittedly, convergence in biological evolution can also produce very close similarities, as in saber-toothed cats and saber-toothed marsupials; but this similarity results from the entirely independent evolution of similar morphological designs, presumably to serve closely similar functions. Neither the structures themselves, nor the underlying genetic information, are homologous in the sense of being derived from a common ancestor. The opposite holds for the transmission of material cultural information—where "theft of idea" is rampant, and much more common than the truly independent invention of closely similar novelties.

2.3. Implications for Classification

In biological evolution, true hybridization interferes with the generation of regularly nested sets of taxa (species within genera, within families, within orders, within classes, and so on) which could be seen as more and more inclusive "packages" of genetic information. True hybridization is

perhaps first achieved, as usual, by the Besson company in Paris, whose "Spécial" model remains so far known only through advertising. Right at the turn of the century, versions of this design were proposed by many manufacturers, including Boosey & Co., Boston, King, Holton (with the first of several models called the "New Proportion"), Lyon and Healy, Thompson and Odell (European import), and York ("The Monarch-New Model"), plus Bohland and Fuchs and other European makers whose instruments were sold in the United States under a variety of names ("stamp horns").

more common in certain restricted lineages of plants and far less common or much more problematical, from an analytical standpoint, in animals. But lateral transfer of genetic information is rife in the microbial world (Margulis & Sagan, 1986), where patterns of biological evolution might have more in common with those of material culture than otherwise specified in this essay.

Although lateral transfer of material cultural information through "theft of idea" and other means precludes the generation of orderly, non-overlapping sets of descended packages of such information (and therefore a genuinely evolutionary classification of basic cornet styles), at a coarser level progressively inclusive sets of material cultural information definitely exist. Such sets may be delineated in more than one way, however. For example, cornets are soprano brasswinds—brasswinds being a conventionally recognized "family" of instruments that produce sound as a player's lips vibrate against a cup-shaped mouthpiece.[9] Not all "brasswinds" are even made of brass; the Medieval and Renaissance "cornetto" and the serpent (a bass instrument) were made of wood and often wrapped in leather. These instruments obtained passing tones (chromatics) with holes, like a woodwind instrument. The most basic ("primitive") brasswinds are simple tubes, which sound only in the natural overtone series, like a boyscout bugle. These instruments include shofars, other animal-horn-derived natural trumpets, and various ancient instruments—especially the Renaissance trumpet, which later was fitted with one or more holes and/or a slide. Other brasswinds obtain the chromatic scale strictly with a slide, the modern trombone and its Medieval predecessor the sackbut being excellent examples. Still other instruments were valved, and the number of different valve systems that have been tried is rather large. Of the mechanisms common in the early-to mid-nineteenth century, only the rotary and perinet piston valve systems survive.

Such instruments are rather difficult to classify. In a famous picture of King Oliver's Creole Jazz Band (e.g., Giddins, 1988, p. 75), Louis Armstrong is shown with a Conn "slide trumpet"—in effect a miniature trombone, and nothing really like an "English slide trumpet" from the nineteenth century. Does Armstrong's instrument belong with the trombone group or with trumpets? In other words, should we classify all slide brasswinds together, all perinet valved instruments together, and so on? Or should we classify these instruments by, say, the inside shape of the tube—which is in fact what scholars have preferred? It was in shocked disbelief when I first read in Baines' authoritative book (1976) that cornets and trumpets had

[9] Experiments have shown that only the player's upper lip vibrates.

developed ("evolved") separately: cornets by placing valves on post horns, and trumpets by adding valves to, well, trumpets. "True" horns have a preponderance of conical taper to the tubing (starting out small and gradually expanding), yielding a generally "darker" and perhaps mellower sound than comparably pitched trumpets, which characteristically produce a sound with more overtones through a preponderance of cylindrical bore. Trumpets are traditionally played with shallower mouthpieces, as well, which accentuates the differences in tonal colors between the two sorts of instruments. My disbelief in reading Baines's (1976) interpretation of cornet and trumpet history came from my experience as a beginning player in the 1950s, when cornets and trumpets were routinely sold as alternative versions of the same instrument—cornets being shorter (meaning with one extra turn, the total tubing being of the same length for samepitched cornets and trumpets), easier to hold and perhaps to play (to the degree that they retained more conical tubing), but in any case played with trumpet-cup style mouthpieces. I accepted the marketed, *de facto*, and manifestly *planned*, convergence between trumpets and cornets. I since have learned that with the adoption of the trumpet and near-total abandonment of cornets after World War I, cornets became commonly "trumpetized," and marketed simply as easy-to-hold-and-play equivalents of trumpets.

Although theft of idea renders straightforward classification impossible, as the shape of the evolutionary "tree" becomes almost hopelessly complex, its branches thoroughly entangled, a multi-level classification nonetheless remains feasible. Instead of a single taxonomy reflecting the systematic generation of brasswind diversity, what we need is a classificatory scheme with multiple levels and criteria. The multi-versions of hierarchical schemes for any general set of designed objects (nested sets of material cultural information) are all at once simultaneously "correct," and also necessary for a full description of the system.

Interestingly, the sheer existence of multiple sets of hierarchies of packages of material cultural information implies (just as does the simpler, single-system in biology) that cornets, all brasswinds, all musical instruments have indeed had a history (whether or not we wish to call it "evolution"). Of course, we have independent means of knowing that material cultural evolution has taken place; but consider the logical parallel to Darwin's argument that the existence of the Linnaean hierarchy entails biological evolution. The Linnaean hierarchy must be present if life has evolved—constituting, in fact, the central prediction of the very notion of evolution, and firmly establishing the scientific nature of the concept. In a parallel fashion, and given the differences in transmission of material cultural and genetic information, *at least one—but expectedly more than one—set of hierarchies of any large collection of material cultural*

information must be present if such information actually changes over time.

This implication is not a little ironic, considering the creationist claim to the effect that "just as a watch bespeaks the existence of a watchmaker, so manifest design in the biological world bespeaks the work of a Creator." Of course, humans create watches; but watches, if analyzed carefully, will show the same multi-sets of hierarchical patterns of resemblance which are the inevitable stamp of their "evolution," just as the Linnaean hierarchy implies that life has evolved. There is no more independence in the construction of individual watches than there is in the biological world. Even in systems with "intelligent design," the fate (stasis and change) of transmissible information is inherently evolutionary.

3. ON NAIVE SELECTIONISM IN THE BIOLOGICAL EVOLUTIONARY DOMAIN

Evolution is the fate of transmissible information in an economic context.[10] The core articulation of this precept is Darwin's original statement of natural selection, as given in the early pages of *On The Origin of Species*: "As many more individuals of each species are born than can possibly survive; and as, consequently, there is a frequently occurring Struggle for Existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be *naturally selected*" (1859, p. 5).

Darwin made it plain, in this initial statement and in all his subsequent writings, that heritable variations in (what we would now call) phenotype within a population implies that some individuals will be better able to cope with life's exigencies (basically the procurement of energy and nutrients, but also survival from predation, disease, and other ambient hazards). The individuals best suited to cope with such extraneous factors—the ingredients of an organism's "economic" life (Eldredge & Salthe, 1984; Eldredge,

[10] Biological evolution comprises several exceptions to this rather broad generalization. One exception concerns "sexual selection" and related phenomena, where (following Darwin's original formulation: 1871, p. 256) transmission of genetic information is biased purely through differential ability to reproduce, as opposed to relative success in the economic domain. Another exception involves pure chance: For example, getting hit by a car before reaching reproductive age may be a consequence of poor eyesight or judgment, and thus may qualify as a crude form of natural selection. But getting hit by a car out of control is just bad luck—having nothing to do with the victim's "fitness."

1985, 1986)—will have a higher probability of leaving offspring to the next generation. And regardless of just how the process of inheritance works, the recipe for success will be differentially passed along, organisms tending to resemble their parents, having inherited 50% of the genes of each parent in sexual species and 100% of these genes in asexual systems.

In recent years Dawkins (e.g., 1976, 1982), Williams (1966, 1992), and many other "ultradarwinian" evolutionary theorists have deviated rather sharply from Darwin's original formulation of natural selection as essentially differential reproductive success following from differential economic success (Eldredge, 1995). The essence of their claim, embodied in notions like the "selfish gene," is a vision where the genes themselves, or their "vehicles" (Dawkins, 1982: meaning organisms) perpetually struggle to leave as many copies as possible of themselves (in the case of "selfish genes") or of their genes (in the case of organisms) to the next generation. It *seems* to us that organisms compete for food—but, in the Dawkins version, food is really not what the competition is about. Organisms rather compete to feed their deeper desire to leave as many copies of their genes to the next generation, the need to leave such copies causing them to compete for food. Whereas Darwin's view of natural selection sees the competition for limited resources as having a side effect on reproductive success, in the ultradarwinian version the causal vector is reversed: Organisms compete to leave their genes behind, forcing them to compete for limited resources. Thus evolution in this view is not a passive "what-worked-better-than-what" ledger book recording the vicissitudes of genetic information in an economic context, but instead an active process of genes jockeying for position—a vision of activity that superficially resembles processes studied in other fields of science. Not for nothing do I see ultradarwinians as suffering from "physics envy."

The connection that Darwin so clearly forged between heritable information and the economic concerns of organisms (a connection that presages a still deeper understanding of the connections between the physical world of matter in motion, the structure of ecological systems, and ultimately the fate of genetic information) is thus obscured by the nearly exclusive emphasis on genes in many quarters of recent evolutionary biology. We must ask, however, if even a more traditional, Darwinian view of natural selection that sees relative reproductive success as the statistical outcome of relative economic success (among conspecifics in resource-limited populations), can adequately explain the diversity and the many patterns we see in the 3.5 billion-year history of life. For the core of evolutionary theory, despite its many nuances, has remained one of *extrapolationism*: We understand the core deterministic mechanism underlying adaptive change (this mechanism being natural selection), and then we simply allow this motor of adaptive change to run through the vastness of

geological time. Evolutionary biology, however, has yet to thoroughly examine the characteristic patterns in the history of life, many of which are cross-genealogical, affecting many unrelated lineages within single ecosystems or regional biotas in a concerted, nearly simultaneous fashion.

Hence the dangers of naïve extrapolationism in evolutionary biology. Because evolutionary theory to date has paid insufficient attention to the repeated patterns in the history of life, a theory has been fashioned, little changed in essence since Darwin's day and in fact further removed from the realities of the physical world, that is ill equipped to explain even the more fundamental aspects of evolutionary history. This is what I mean by naïve selectionism—the simple assumption that, left to its own devices, natural selection will, over geological time, inevitably produce adaptive evolution.

3.1. Evolutionary and Economic Hierarchies

The outlines of a much more richly descriptive evolutionary theory are now becoming clear (Eldredge, 1999). It is based on two converging sources: one quite abstract and theoretical (though itself a good description of the structure of biological systems), the other more intensely and purely empirical.

In brief, the more abstract component sees the biological world as structured in two separate, though interactive, hierarchical systems. One is the "evolutionary" or "genealogical" hierarchy of genes/organisms/demes/species/monophyletic taxa. Focusing on elements of the genealogical hierarchy has been natural to evolutionary theorists. Specific entities at each level engage in "more-making" behavior: organisms reproduce, with replicative fidelity supplied by their genes; ongoing organismic reproduction keeps demes going; the fissure and merging of demes keeps species going; and speciation (the production of two or more descendant species from an ancestral species) is what keeps monophyletic taxa going through geological time. No more speciation, and ultimately even phyla will disappear!

That the ecological realm is also structured into parts and wholes has been less well appreciated. Whereas "more-making" is what holds together the "wholes" of the genealogical hierarchy, in ecological hierarchies the interactive dynamics among components that form the next-level cohesive wholes involve matter-energy transfer. Conspecific organisms in local populations (in an ecological sense, "avatars:" Damuth, 1985) variously compete and cooperate for energy resources. Up one level, *among* avatars, a spectrum of weak (or neutral) to strong interactions applies, as carnivores eat herbivores, which eat the plants supplying the energy to the ecosystem at its core (through photosynthesis). The term "ecological niche"

conventionally describes the role played by each local avatar in matter-energy transfer. It is the flow of matter and energy among avatars that, on a moment-by-moment basis, defines and integrates the local ecosystem. But matter and energy flow—sometimes as leakage, sometimes strongly directional across local ecosystemic boundaries—links local ecosystems up into regional biotas ("biomes") and, ultimately, into the grand global ecosystem that is sometimes called "Gaia." Just as all life forms a (curiously unnamed) super-taxon, all of the world's ecosystems are interconnected as part of the global matter-energy flow.

Organisms thus engage in two, and only two, fundamental classes of activity. They obtain energy and nutrients in order to differentiate, grow and maintain their living selves—their *economic* behavior. And they reproduce, reproduction being contingent on successfully carrying out the first class of activity (the converse being manifestly untrue). As a direct consequence, organisms find themselves engaged in two distinct kinds of larger-scale systems. On one hand, organisms are members of local populations in an economic sense (avatars), which are parts of local ecosystems, which are in turn parts of regional systems, and so forth. And as reproducers, organisms are parts of demes, which are parts of species, which of course are parts of taxa of higher categorical rank.

3.2. Core Patterns in Biological Evolution

Darwin's original formulation points to natural selection as the main, most obvious connection between the economic and genealogical hierarchies. But natural selection, seen as a bridge between the ecological and genealogical hierarchies, does not entirely address how the two hierarchies interact to yield evolutionary history—as even a cursory examination of repeated patterns in the history of life makes clear. A spectrum from local ecosystemic disturbances up to global mass extinctions shows how events in the physical world, acting at varying spatiotemporal scales, actually drive the evolutionary process (see Eldredge, 1999, and in press, for details). By "drive" I essentially mean "control," as adaptive change seems to be infrequent within the history of species lineages—long periods of quiescence or evolutionary "stasis" being interrupted by occasional spurts of adaptive change generally associated with true speciation (the pattern underlying the original formulation of "punctuated equilibria:" Eldredge & Gould, 1972).

More recently, it has become abundantly clear that the speciation events that interrupt periods of stasis in individual lineages are random neither with respect to environmental events nor with respect to patterns of stasis and change in other broadly sympatric species lineages. Adaptive

change often seems to happen more or less simultaneously in a number of separate evolutionary lineages, in response to physical environmental events of sufficiently great spatiotemporal scale and intensity to trigger biogeographic change, extinction, and true speciation (see Ivany and Schopf, 1996 for an entire volume of case histories). The latter pattern of ecosystemic disturbance, biogeographic change, extinction and speciation affecting many different lineages near-simultaneously has been variously termed "turnover pulse" (e.g., Vrba, 1985) or "coordinated stasis" (e.g., Brett & Baird, 1995).

Stasis, speciation and turnover pulse/coordinated stasis seem to constitute the three fundamental patterns of evolution seen in the fossil record (Eldredge, in press). By *pattern*, I mean almost hauntingly similar aspects of the histories of species-lineages throughout the one and a half billion years of the history of multicellular life. Stasis and speciation were as typical of the histories of Cambrian trilobites as of Plio-Pleistocene hominids. And, turnover-pulse or coordinated stasis were named for ecosystem-wide regional events in the Pliocene of eastern and southern Africa, and for a series of eight successive faunal regimes (each about 5–7 million years in duration) from the mid-Paleozoic of eastern North America. Other evolutionary patterns do occur, however, and are important to a full consideration of how life evolves. For example, although stasis has empirically emerged as far more common during most of the history of most species lineages, *phyletic gradualism* (gradual transformation within lineages) also happens. So do *adaptive radiations*—in my view, much neglected in evolutionary theory since last examined seriously in the mid-twentieth century.

Note that the three core patterns of stasis, speciation and coordinated stasis/turnover pulse are essentially "additive" (Figure 5): One can depict stasis wihin a single species lineage by a single, essentially vertical line (Figure 5A); speciation by the addition of one or more vertical lines (Figure 5B); and coordinated stasis/turnover pulse by a whole series of such lines, each individual or cluster representing different species lineages (Figure 5C). Together, the three patterns specify the conditions under which adaptive change through natural selection actually occurs in the evolutionary process.

3.3. Environmental Disturbances and the Core Patterns

Elsewhere I have discussed a series of spatiotemporal levels of physical, environmental events with ecological and evolutionary effects (see Eldredge, 1999, in press). Starting from the lowest level and working up:

1. *Environmental stability*: In this "null" condition, environmental fluctuations and perturbations lie entirely within the "expected"

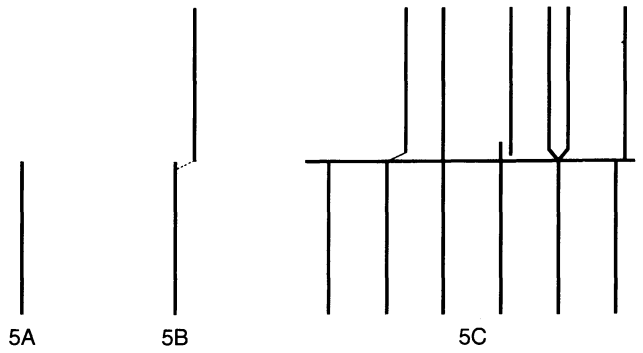


Figure 5. Three basic patterns in the history of life, commonly encountered in the fossil record. Panel 5A depicts stasis, the relative anatomical stability within a single species through time; the solid vertical line subsumes whatever within-population and geographic variation may be present (at any one time, this variation may be substantial). Panel 5B represents speciation, whereby a descendant species derives from an ancestor; the record may or may not reveal stratigraphic (that is, temporal) overlap between the ancestral and descendant species. Panel 5C depicts a "turnover pulse" event; many separate lineages within a regional ecosystem, all originally in stasis, variably undergo extinction, survival, or speciation. The three patterns are "additive," 5C comprising many near-simultaneous instances of 5B, which in turn consists of two species in ancestral/descendant relationship, both in stasis (5A). For further explanation, see text and Eldredge (in press).

range of all populations of all species living in local ecosystems and regional biotas. Diurnal and seasonal fluctuations (typically greater in the higher than lower latitudes for many environmental parameters, such as ambient temperature), are within the expected range of tolerance of all resident species. Anatomical, physiological and behavioral adaptations are in place. One would expect stabilizing selection with respect to such adaptations, with little or no species-wide accrual of adaptive evolutionary change.

2. *Local Succession*: When environmental perturbations exceed the normal tolerances of local populations, individual organisms die off. Examples include migrating sandbars eradicating benthic invertebrate fauna of a portion of Tomales Bay, California (Johnson, 1972); prolonged exposure of sessile intertidal organisms due to abnormally lengthy low tides; Hurricane Hugo damage to Puerto Rico, 1989 (see Eldredge, 1999, Ch. 1); wildfires; and so forth. These events are sufficiently local that entire species are not eradicated. "Recruitment" from outlying demes (conceived as reservoirs of genetic information) supplies the organisms that rebuild the local

ecosystem, usually in a fairly orderly sequence from "pioneer" species through those species characteristic of the mature ecosystem. Such a process of "ecological succession" uses existing reproductive and economic adaptations; thus selection remains stabilizing and little evolutionary change is expected to accrue.

3. *Regional habitat tracking*: Larger-scale environmental change overwhelms the adaptations of the components of regional biotas (that is, many geographically adjacent local ecosystems). However, rates of change do not overwhelm the capacity of the great majority of local populations of species *to track and occupy habitats to which they are already adapted.* The classic example is the migration towards the tropics of biomes (tundra, boreal forest, mixed hardwoods, etc.) during times of glacial advance, and *vice versa.* Species tend to remain stable in the face of environmental change even of this magnitude; succession occurs laterally, and natural selection remains dominantly stabilizing when summed over the populations of entire species.
4. *Threshold: turnover pulse/coordinated stasis*: When regional perturbations become so severe that they overwhelm the capacity of many species in a regional biotic system to find familiar habitat elsewhere, these species suffer extinction. In addition to succession and stability for some species (that disappear from, or enter into, the region), genuine extinction *and speciation* take place. Selection is directional, while evolutionary novelties evolve relatively rapidly in conjunction with the origin of new species. Vrba's (1985) account of events in eastern and southern Africa 2.5 million years ago is a classic example of turnover pulse/coordinated stasis.
5. *True mass (including global) extinction*: At the highest spatiotemporal levels, global mass extinctions (whether occasioned by global climate change, extraterrestrial bolide impact, or other physical causes) profoundly disrupt ecosystems in virtually all regions and regimes, from the higher to the lower latitudes, in the oceans as well as on land. Higher taxa (the larger-scale "packages" of genetic information) become extinct. *Accordingly, evolutionary radiations of lineages often produce roughly equivalent sized packages of genetic information.* For example, mammals originated in the Upper Triassic at about the same time as the dinosaurs; but they did not radiate into a diverse array of taxa and did not fill a wide variety of ecosystemic roles until the terrestrial dinosaurs, along with many other taxa, finally became extinct at the end of the Cretaceous Period.

This spatiotemporal spectrum of physical environmental events, the degree of ecosystemic disturbance they cause, and the subsequent loss and evolution of packages of genetic information (taxa of various categorical rank, from species up through phyla), is itself hierarchically arranged and corresponds very closely to the general (albeit more abstract and formal) description of the parallel ecological and genealogical hierarchies. No disturbance, no evolution; disturbance of local ecosystems results in orderly recruitment of organisms from neighboring demes; with more regional disturbance, the succession becomes lateral (as entire biomes move). At the regional threshold level, all the above processes continue, but extinction begins to claim entire species and disruption spurs other species to split—a basic necessity for most of the genesis of adaptive change in evolution. Finally, at still larger geographic levels, the rare events that throw the majority of the world's ecosystems into paroxysms of disruption cause the disappearance or the consequent radiation, if not the actual origin, of larger-scale taxa.

I have called this give-and-take between ecological and genealogical systems (triggered always by external, physical environmental events) the "sloshing bucket" model of evolution: the more profound the physical event, the more encompassing the ecological disturbance, hence the more genetic information is lost—with a correspondingly greater degree of evolutionary activity set in motion. The "bucket" is formed by these two hierarchies sitting side by side—created by the simple fact that organisms simultaneously engage in economic and reproductive behaviors.

4. EVOLUTION OF MATERIAL CULTURAL INFORMATION

Very useful parallels can be found between the "sloshing bucket" model of biological evolution (Eldredge, 1999, in press) and patterns of stability and change in the history of particular systems of material cultural information. For a system like that of "brasswinds," or even a restricted subset of it such as the "cornets," lateral information transfer probably implies the existence of more than one informational hierarchy. But regardless of the number of hierarchies, a history of stasis and change in material cultural information ensures that it is hierarchically structured as surely as is evolution in biological systems.

4.1. Informational Hierarchies

What are the "fundamental units" of material cultural information? I have toyed with the notion of memes as the information-underlying

components of cornet design—for example, fixed leadpipes vs removable shanks; position of the third valve slide *vis a vis* the leadpipe; etc. But quasi-discrete cornet *models*, such as the two variant models of the "Courtois" or the Besson "Concertiste" and "Desideratum," can also be defined and recognized with a fair amount of precision. Futhermore, many of these more "successful" designs were made (with minor variations, to be sure) by a number of rival manufacturers, though some makers maintained either their own uniquely specifiable models or highly distinctive versions of the more common models. This suggests to me—in, I must emphasize, a very loose and informal sense—that basic cornet designs are essentially "packages" of material cultural information similar to species in the biological realm. Species are held together by the exchange of genetic information; put another way, species are the largest sets of sexually reproducing organisms whose members all share a "Specific Mate Recognition System" (Paterson, 1985)—a set of anatomical, physiological and behavioral adaptations that allow them to treat one another (across sexes!) as appropriate mates—a fertilization system in the broadest sense. Cornet models, by contrast, are "held together" by a type-token relationship where new individuals are produced by direct manufacturing from an example and/or a set of specifications.[11]

I do not want to be overly rigid in suggesting an analogy between fundamental cornet designs and biological species. One might reasonably argue, for example, that the Courtois design was actually copied by two important American manufacturers: the Conn company, which made versions of both Courtois sub-models (the two "Wonder Models," seriatim, from roughly 1886–1903), and the Boston Musical Instrument Manufactory, which produced a double water-key cornet from ca. 1869–1910.[12] Although species are often difficult to classify—and biologists sometimes still argue whether a given complex includes one large, variable species, or several closely related, similar species—deeper ontological problems may well lie in making the equation between biological species, on the one hand, and basic design units, on the other.

[11] Of course, many manufacturing concerns do both. I am in possession of the shop model—the "type"—of a Concertiste-style cornet from the Evette and Schaeffer company, a Parisian concern better known for its woodwinds, but that also made cornets and other brasswinds from ca. 1895–1905. Modern manufacturers, such as the David G. Monette Corporation of Portland, Oregon, likewise maintain "shop horns" for producing suitable mouthpieces, and (augmented with detailed written specifications) producing additional specimens of the model itself.

[12] When it moved in ca. 1902, this company became the Boston Musical Instrument Company, and shortly thereafter (no later than 1908) added a fixed leadpipe and "quick change to A" slide to its famous "Boston 3-Star" cornet—finally dropping the double water key that had been on all their perinet Bb cornets since 1869. Dates are based on the unpublished research of Robb Stewart of Arcadia, California.

Yet in one way cornet "models" are indeed very much like biological "species:" Because most models were made by more than one maker, the material cultural information underlying any particular model is, in effect, "broken up" and distributed among different manufacturing concerns—much as species are "broken up" and distributed, as "avatars," into different local ecosystems. And, just as the mutational, selectional, and other dynamic aspects molding the fate of genetic information within local populations must differ among populations and ecosystems, the fate (design stability or change) of the material cultural information underlying within-firm manifestations of a basic cornet design is also bound to differ.

4.2. Economic Hierarchies

Is there a corresponding *economic* system, perhaps also hierarchically structured, and in important ways "decoupled" from the pure hierarchy of material cultural information? Is there, as is the case with multi-hierarchies of material cultural information, more than one economic hierarchy pertaining to any one system of production (of brasswinds in general, or of cornets in particular)? In a general sense there must be, if only because all manufacturing is by definition quintessentially "economic." But what is the general structure of the manufacturing system that enables and constrains the actual production of instruments following the basic designs underlain by material cultural information?

Human social systems are hierarchically structured (cf. Crumley, 1995). If an individual is a member of a single family (genealogical system), he or she is also a member of many different sorts of economic structures variably construed as "political," "social" or "economic" in the purest sense: People live in neighborhoods, within villages/towns/cities, within counties/states/countries, etc. At the same time people may belong to a church, itself affiliated with other churches, and so forth; they may belong to the scouts, an organization that is itself hierarchically structured at the local, regional, and national levels; and they may be employed. All of these systems are non-genealogical and pertain directly to aspects of a person's non-reproductive, therefore "economic" life. Some, such as employment, have direct relevance for reproductive success, whereas in others like church-going the economic nature of the interaction may be muted—but is nonetheless always present.

As far as cornets are concerned, it is the realm of manufacturing firms, by definition "economic entities," that concerns us. Firms, especially nowadays, may be actually parts of larger organizations ("corporations") or may be wholly independent. Firms are, in many ways, like the local ecosystems including a number of populations drawn from various species. In local

ecosystems, individuals variably compete and cooperate for energy resources; within firms, the production line, no matter how standardized, creates variability in the "same" product from item to item. The type-token process of production simply can not produce exactly identical items time after time, no matter how standardized the production process.[13] Any competent musician will confirm that no two horns play alike, and a customer is always well advised to "play test" as many different horns of the model desired before making a purchase. Thus horns vary, and in a sense compete *within single models within single firms*—as their variable properties will cause some horns to be "selected" over others (though tastes vary among players!). In this sense, individual horns are like individual organisms, and production runs of the same model constitute local populations of a model within the context of a single firm.

Furthermore, rarely did a company produce only a single *model* of an instrument in the history of cornet manufacture. This is especially true of the larger firms, with a higher rate of cornet production.[14] Judging from its

[13] The Besson Company of Paris was one of the first, if not indeed the earliest, to use steel mandrels to standardize the production of the parts of its instruments—a process they proudly called "Système Prototype."

[14] In their heyday, the arguably premier makers (judging by their prices and the use of their models by professionals) in both France and the United States heavily focused on a single basic model. Courtois in France made its two versions of what was really the standard cornet design in the latter part of the nineteenth century, roughly from the years 1860–1900. I know of only a few Courtois "modèle français" instruments—cornets where the bell and the lead-pipe are both on the right side of the valves. All of Courtois's other cornets were either type A or B (as shown in Figure 3), though these models were ultimately offered in three different "bore sizes" (diameters of the tubing, as measured at the valves).

The Boston company presents a slightly different story. Restricting ourselves to the Perinet valve instruments, Boston made one essential, characteristic design from ca. 1868–ca. 1900, the model construable either as a variant version of the double-water-keyed Courtois or as a distinct model in its own right. The older instruments were 0.485″ bore, a design that persisted essentially unchanged through the later 1870s–1900 as the "Two Star." At some point in the 1870s, they introduced a model with a smaller bore size (0.475″), a slightly brighter-sounding instrument which they named the "Three Star," and which became their flagship model. These two (in effect, sub-models) were sold for the same price, the Two Star sometimes advertised as the "orchestra" model, with the brighter Three Star for solo and band use (generally outdoors).

But that is by no means the whole story of competition among designs *within* the Boston Company. The company was founded when three persons bought out the manufacturing concern of Elbridge G. Wright, one of the earliest high-quality manufacturers of American brasswinds. Wright stayed with the newly named "Boston Musical Instrument Manufactory" for about one year before moving on (R. Stewart, personal communication). Wright's production mainstays had been keyed bugles and rotary valved cornets. Yet keyed brasswinds, as opposed to rotary valved instruments, were for all intents and purposes "extinct" by the late 1860s. That there was a genuine competition between rotary valved and perinet instruments within this single, high-quality manufacturing company becomes clear from the

advertising and price lists, the Besson company had as many as seven or eight cornet models for sale from the early 1870s through the 1920s, though evidence from the horns available suggests that only a progressively changing subset of these models were actively produced throughout that period (Eldredge, unpublished ms. A). Likewise, the American firm founded by C. G. Conn produced no fewer than four distinctly different models in the early 1900s.

In a very real sense, therefore, multiple *models* from a single shop compete with one another, though the models are often differently priced. According to pricelists from 1893 and 1910, no two Besson (Paris—the family had sold off the London branch in about 1895) models were sold for the same price; yet all their instruments were of very high quality and excellent players regardless of price. Obviously, diversity of product line is one strategy to reach a larger market share, a strategy more open to larger firms than smaller ones, with limited production aimed solely at the high end of the market.

The whole market, of course, is the economic arena we immediately think of when discussing competition. Competition among firms for market share in the broader "ecosystem" of musical instruments/business/marketplace is the quintessential level for clear analogies with hierarchically arranged ecological systems. The hierarchy of manufacturing thus includes much more levels than the biological realm of organisms/avatars/local ecosystems linked by matter-energy transfer. The hierarchy of individual cornets/models/firms/marketplace is more complex than the biological hierarchy; and it is the marketplace, rather than the firm, which most closely corresponds to the "local ecosystem" of biology.

The inherently more complex structure of "competition" in the world of material cultural information also deserves emphasis. Competition underlies any model of selection. What does the competing in material cultural evolution? In a sense, individual *horns* compete within the shop where they are produced; different *models* within a shop also compete; *firms* surely compete, and, in terms of their products, compete by producing a variable

almost poignant rhetoric in some of their catalogues. Noting that the French had essentially gone wholeheartedly to perinet valves, while Germans and Americans still preferred the rotary (by the 1870s almost surely a hollow claim as far as American players were concerned), they bravely (or stubbornly) continued to offer four small Eb rotary valved cornets ("top action" vs. "side-action" in two different bore sizes), as well as four Bb rotary valved cornets (partitioned the same way). By the late 1870s, however, they came out with a truly novel model, a Bb cornet formally named the "1879 Patent Model" (also sometimes called the "Three Star"). This truly remarkable instrument represents the Boston company's last-ditch effort to produce a rotary-valved cornet that had the look and feel of a perinet-valved instrument, but with the shorter stroke of rotary-valved instruments (which allowed quicker fingering). The 1879 Patent Model, a wonderfully designed horn that plays fantastically well, and obviously designed in the hope of pleasing the public, was by all signs a commercial flop.

array of the "same" model, as well as an array of different models.[15] Thus many manufacturers emulated the basic Courtois design, all claiming parity of quality. Courtois knockoffs (some quite good, others very poor, and all invariably sold at a lower price) were rife. The makers wanted the public to think they could pay less and get the "same" instrument through some superficial resemblance. Judging by the number of such horns still around, this strategy was not wholly unsuccessful (although the real players always knew who made the good horns).

However, firms do not compete strictly through their products. They employ different capitalization resources, different advertising and marketing strategies. Little firms seem more vulnerable than bigger firms, often regardless of the models they produce or of the quality of their instruments. Some firms are simply better managed. Some are just luckier. Clearly, no model of "naïve selectionism" (no simple "build a better mousetrap and the world will beat a path to your door") will ever suffice to explain more than a relatively small fraction of the actual case histories of stability and change of designs, underlying information, and manufacture of any class of artifacts, from Paleolithic stone tools to computers, including cornet design history.

Finally, still higher levels of economic organization directly affect the fates of material cultural information: local, regional, national, increasingly multi-national (such as the European Economic Union) and, ultimately, "global" economic forces. Depressions put companies out of business as surely as comets wiped out the last dinosaurs; no matter how good their products, companies can be overwhelmed by some higher-level catastrophe and succumb. Thus the fate of material cultural information, itself complexly structured in a multi-hierarchical array, appears to be governed by events in an economic sector that is also complexly and hierarchically arrayed. Biological evolution and the fate of sets of material cultural information through time are similar at a gross level, although the complexity of the human manufacturing domain is many times greater than that of the biological.

4.3. Core Patterns in Design Evolution

The historian F. J. Teggart (1925) pointed to three basic patterns that he felt were general in cultural evolution. For Teggart, a theory of

[15] When faced with a supply of produce greater than they can sell, the firms that specialize in packaged food (e.g., frozen peas, spinach, etc.) tend to distribute the extra supply as house brands—giving the consumer a choice between two identical products at different prices, and in a sense competing with themselves—though obviously realizing more profit than by simply wasting the extra supply. Much the same happens with name-brand versus "generic" drugs.

"cultural evolution" should describe "how things have come to be as we find them today." His three patterns correspond closely, albeit not exactly, to the three core patterns specified above for biological evolution. In order of importance in the shaping of human history, Teggart mentioned (1) gradual "drift" through time, (2) great stability of cultural traditions, and (3) introduction of the truly new, which Teggart saw as arising mostly through the collision of cultures—as when "Hyksos" invaders, whoever they may have been, invaded ancient Egypt bringing the wheel with them.

Teggart equated drift (pattern 1) with what was later termed "gradualism," and which he characterized (in my view correctly) as the predominant expectation of patterns of change in biological and cultural evolution in his day—an expectation that still persists in many circles. Teggart felt that even though some gradual changes, such as drift in pronunciation, spelling and grammar of languages, do occur, gradual change is *not* the true stuff of human history. Pattern (2), cultural stability, is far more common. Patterns (1) and (2) are widely regarded as antonyms; indeed, the very title of the initial paper on "punctuated equilibria" (Eldredge & Gould, 1972) suggested as much.

Re-examining Teggart's proposal in light of the three core patterns of biological evolution, some more detailed and interesting parallels emerge. For example, it has become clear in the years since the original publications on "punctuated equilibria" that instances of gradual change can indeed be found in the fossil record. What has not been recognized until relatively recently (Eldredge, 1995; Lieberman et al., 1995) is that all such published examples—by friend or foe alike—involve only geographically discrete portions of the range of entire species, while the species as a whole remains basically stable. For much permanent change to accrue gradually within a species, that species should be highly localized, in effect reduced to one or only a few local populations.

I see the same thing with cornets. Though most models remain uncannily stable both within and between firms, some noteworthy examples fit the expectation of gradual, progressive change. Of course, models do not gradually change on a day-to-day basis; but minor changes in tubing configuration, for example, have happened (albeit in discrete steps) so often in the history of production that a model of smoothly gradual change best fits the data.

Here I have in mind the cornet production of the Conn Company in the first decade or so of the twentieth century. In the first few years of the twentieth century, Conn introduced three very different models of cornets, all with fixed leadpipes (the company thereafter phased out the production

of a fourth model, the Courtois-like "Wonder," with its design so closely tied to the previous century). Two of the new models, the "Conn-queror" (introduced ca. 1902) and the "Wonderphone" (ca. 1907), are especially intriguing from the present standpoint (Figure 6). Each model name, oddly, was applied to two very differently designed models, viz. Conn-Queror #1 (ca. 1902–1903) and ConnQueror #2 (ca. 1904–1910); and Wonderphone #1 (ca. 1906) and Wonderphone #2 (ca. 1907–1910).[16] *Within* a given submodel, however, especially ConnQueror #2, a progressive change, a nearly constant tinkering with design, can be clearly detected: Conn constantly called their latest models "Perfected" and claimed in their advertising that their latest models were superior not only to those of all other makers, but to the cornets they themselves were producing earlier. One contemplates Conn cornets between 1900 and the outbreak of World War I and thinks instantly of "planned obsolescence." The most egregious example of such "phyletic gradualism" occurred in 1904 and 1905, when no fewer than four different versions of the ConnQueror #2 appeared serially—a modified design every six months or so, each differing from its predecessor by minor changes in the angle of some of the tubing between the three valves.

Yet Teggart is right: Such minor changes, no matter how progressive, are *not* the stuff of true design innovation—whether for Conn's Conn-Querors and Wonderphones, or any other cornet model known to me. The basic signal, instead, is great stability of design—as with the Besson Desideratum, the Concertiste, the two variant versions of the classic Courtois, the Boston cornets, etc. True design change, when it does come, seems to be abrupt—the introduction of a wholly new model involving a distinct configuration loosely tied to the maker's previous designs, to other designs, or even inspired, in Lazarus-like fashion, by designs that had been dropped for a number of years.

What are the circumstances that prompt such changes? Is there any analog of true "speciation" going on in design history? One possible example of such a speciation event is the change from the early version of the French Besson Concertiste to the later version, replaced (in 1888

[16] These informal designations are mine, and this simple classification actually obscures some of the documented variation; the dates of manufacture of the different models and styles are based on unpublished data drawn from collections and advertising. Both Conn-querors, while radically different from each other, were characterized by unusual connections of the windway between the valves. Both versions of the Wonderphone (also quite different from each other) retained elements of a much earlier and very rare Conn cornet with bell tuning. See Banks (1994) for illustrations of the Connqueror #1 (p. 38) and #2 (p. 39).

Figure 6. The three cornet models offered for sale by the C. G. Conn Company in 1910. All three models have fixed leadpipes, and all are heterodox designs *vis a vis* traditional 19th-century designs (cf. Figures 1–4). All are "perfected." These "Wonderphone" and "Conn-queror" cornets both exemplify the second models to bear such names (see text). Advertising postal card in the author's collection.

and 1889, respectively[17]) by two very similar descendant models: a later "Concertiste" (1888, see Figure 1), now the most expensive model in the Besson stable, that differed in consistent but not major details from the earlier, unnamed version; and the "Soliste" (1889), which retained the basic accouterments of the older model, but with a different configuration of tubing between the valves, becoming the third most expensive Besson model after the Desideratum.

What was going on in the late 1880s in the Besson firm? According to Waterhouse (1993, p. 30) and my own data (Eldredge, unpublished ms. A), these new designs appeared just when the Besson company registered its new trademark, "Système Prototype," in 1887, changing the stamping on the bell and adding the initials "S. G. D. G." (for "sans garantie du gouvernement"). Two years later the company moved, from 92 to 94–96 rue d'Angoulême. Of course these bare facts are by no means definitive. But whatever the changes in the fortunes of the company might have been in the late 1880s, they seem to have been correlated with, and they perhaps even prompted, the appearance of two new models—both derived from a single design that had been in use since the early 1870s.

A further example of design divergence involves a higher level of economic organization. The French Besson family sold their London operation in 1895. The new owners began, not long after the turn of the century, to add a fixed leadpipe to the Desideratum model and to make a longer bell (eliminating the "shepherd's crook" bend at the rear of the bell that was so characteristic of the vast majority of nineteenth-century cornets). It is as if the corporate split prompted the new owners in London to tinker with the design of their inherited Desideratum model; indeed, they became so confused that they brought out a "new Desideratum" in 1911 that was in fact a "Concertiste" according to the original model French name.

Thus changes in design seem to be spurred by changes in economic circumstances: a new management, new quarters, and undoubtedly, hiring or otherwise hooking up with new talent, as the Besson company reportedly did in 1867 (when Gustave Besson worked with a M. Girardin "over a new series of brass instruments:" Waterhouse, 1993, p. 29). But these design changes occur independently of individual manufacturing concerns—as in the "random" speciation model that has been prevalent in evolutionary biology until very recently, when it became apparent that speciation is commonly correlated among lineages living in the same region. Is there anything like such concerted changes in cornet history? The answer

[17] Information based on 1893 catalogue copy (p. 9) of the "Fils d'Eugène Thibouville," a company that also sold Besson instruments.

is yes—as the following thumbnail sketch of cornet history makes abundantly clear.

5. THUMBNAIL SKETCH OF CORNET HISTORY: COORDINATED STASIS/TURNOVER PULSE OF MATERIAL CULTURAL INFORMATION

Traditional evolutionary analysis, for good and sufficient reason, studies distinct lineages—examining hierarchically nested patterns of genetic information as they develop through time. Ecological analysis, on the other hand, focuses on cross-genealogical systems, generally as they are structured through internal dynamics of matter-energy flow on a moment-to-moment basis. Both approaches must be integrated to arrive at the "sloshing bucket" model of evolution, and to uncover the nature and significance of extinction, rapid evolution, habitat tracking, and coordinated stasis/turnover pulse.

A similar remark holds for the evolution of design. Important as it is to trace the history of individual designs and to chart the course of individual manufacturing firms, the more general patterns of cornet design "evolution" emerge only by stepping back and looking at the industry as a whole through the latter two-thirds of the nineteenth century up to nowadays. What follows is a necessarily very brief capsule history.

5.1. Origin and Early History

According to Baines (1992, p. 81), the cornet was invented by the French maker Halary in approximately 1828—by adding valves to pre-existing natural horns, as already mentioned. The early cornets had Stolzel, not Perinet valves. Though some perinet-valved cornets are known from the 1840s (e.g., by Adolphe Sax and Gautrot), the dominant soprano brasswinds were equipped with Berliner, Vienna, Stolzel or rotary valves until approximately the mid-1850s, when Courtois, Besson and other mainly French makers gained a foothold with their perinet models. Many of the early perinet cornets I have seen from this period (mid-1850s–1860s) are "modèle français," the bell appearing to the right of the valve assembly, as in Stolzel-valved cornets (also known as "cornopeans"). Indeed, a Courtois made between 1856 and 1858, and currently in a private collection, shows the usual configuration of a cornopean but with perinet valves—very much a

transitional ("missing link") design; it is an instrument apparently made under license from Sax.

5.2. 1860–1900. The Great Age of Victorian Cornets

Besson, Gautrot, many other French makers and some English manufacturers as well (English Besson, Distin) continued to make French-style cornets at least until 1900; Gautrot's successor, Couesnon, made them even after World War I. However, the orchestra leader and instrument dealer Jullien, together with his famed cornet soloist Koenig, introduced "English model" Courtois cornets to London in the late 1850s. (In the English model, the bell appears to the left of the valves, as in all conventional modern cornets and trumpets. The oldest true "modèle anglais" perinet-valved cornet that I have yet found is the "Nouveau Modèle" of Antoine Courtois, the one example I have seen [serial no. A712, author's collection] made no later than 1855.) Two different "Koenig" Courtois models are known—one quickly disappearing, leaving the instrument depicted in Figure 3A. Along with the variant model depicted in Figure 3B (usually known as the "Arban" model, but sold under the name of other soloists as well), this Courtois design embodies *the* classic Victorian cornet. Very few "French model" cornets from this period turn up in England and North America, and the "English model" dominated cornet sales in France as well: I have located only one single "modèle français" Courtois cornet from this period.

Meanwhile, the French Besson company added English model cornets to their line at least by the early 1870s: These models were the Desideratum, also available in the French configuration, and the early Concertiste. Most of their surviving instruments from the 1870s onwards are English-style, which their price lists consistently show as more expensive, hence better, models. The Boston Musical Instrument Manufactory, on the other hand, began operating in 1869, offering an early version of their classic double-water key cornet. The Conn firm (initially Conn and Dupont: see Banks, 1994, p. 1; Waterhouse, 1993, p. 70) began producing cornets in 1876, first offering a complexly designed "Four-in-One" Model (playing in high Eb, C, Bb and A), and then, by 1881, a somewhat more simply designed C-Bb-A instrument (under the name C. G. Conn alone), along with a separate Eb model; the first of their two Courtois-like "Wonder" models did not appear until ca. 1886. Between 1879 and 1886, Conn produced copies of both the Besson Concertiste and the Besson Desideratum, but apparently in very low numbers.

These different models exhaust major design variation; all other makers produced variant versions, from sheer replicas to models only

slightly deviant from these few basic, now "classic," English-style designs. (I have listed most of the major manufacturers, and the models they produced, in footnotes pertaining to the three major early *modèles anglais* of this period.) Very little experimentation and design innovation occurred from the early 1870s until about 1900, the most basic design of all being the Courtois model developed in the mid-1850s.

Thus the second phase of perinet cornet history, running from ca. 1860 to 1900, was one of initial development of a few basic, highly distinctive models—which were then copied by all other manufacturers, regardless of when the other companies became established. Anomalies occasionally show up, but are the exceptions that prove the rule. And whereas no single big economic factor may have triggered the rise of English-style cornets (aside from the high quality of the instruments themselves), modèle anglais instruments were put on the map in London by the promotional efforts of Jullien, closely followed by his successor, the musician and dealer S. Arthur Chappell.

5.3. 1900–1920. The New Era

Something happened right at the turn of the century that radically changed the cornet design landscape. The French Besson company's production of cornets suddenly dropped from ca. 2000 a year (maintained on the average for at least the previous thirty years) to around 1000, and two French manufacturers either went out of business entirely (Ouvriers Réunis) or stopped making brasswinds (Evette and Schaeffer, both ca. 1905). Yet I did not find any concrete evidence that general economic conditions in France, or Europe in general, or in the United States, prompted these events. I am left speculating that it was purely a desire to modernize, to drop the symbols of the previous century and come out with a "modern" horn—a desire prompted by the calendar change from 1899 to 1900—that galvanized major changes in cornet design just a few years before the turn of the century.

Courtois apparently stopped making its famed early models (Figures 3A and 3B) a few years after 1900. The Boston Musical Instrument Manufactory changed its name (to "Company") and its address in 1903, still making the piston-valved "3-Star," though some instruments had longer bells. Soon, the company was also making a fixed leadpipe-quick pull to A (very like the instrument depicted in Figure 4). To my knowledge, its last cornet design was a long-bell model still called the "3 Star," but quite unlike the original, classic cornets bearing that model name.

In the place of these nineteenth-century stalwarts came a rash of novel designs. I have already mentioned one particular event—the application of

fixed leadpipes—with a number of alternative means of effecting a "Quick Change" in pitch (generally between Bb and A). The most widely emulated was the fixed leadpipe version of the "Fin de Siècle" model (Figure 4). Other models included the two ConnQuerors and Wonderphones of the Conn company.

Long-bell cornets were "in," most without the old-fashioned shepherd's crook—which, along with the extensions of the bottom valve caps, came to symbolize the outmoded designs of the nineteenth century. An early example of the new models was Conn's "Perfected Wonder" (see Figures 6 and 7), with its fixed leadpipe curved into the shape of a backward S—a design they may not have invented and that was made by many companies, European and American alike. In addition, the Holton company, Standard Band Instrument Company, York, and Buescher all brought out their own designs of long-bell models. This wave of innovation touched off a frenzy of copying. For example, the eastern European manufacturer Bohland and Fuchs, already well established as a maker of the classic designs, started copying all these later designs as well—even such arcane models as the York Perfectone.

World War I generally halted production of cornets in France, but seemed to have had little impact on American output. (The United States, after all, was only actively involved for a single year. Word War II had far greater impact on the production of brass musical instruments). Factors other than the World War I brought this third phase to an abrupt close around 1920.

5.4. 1920–1985. Cornet Eclipse

In the late nineteenth century, there were over 10,000 town bands in the United States, and perhaps four times that many in Great Britain (Hazen & Hazen, 1987, p. 8). Yet by 1915, the musical instrument business was undergoing a sea-change. The reason: Town bands, nuclei for so much of the entertainment in American towns, had all but disappeared, victims of the rapid spread of radios in American homes. In the 1920s, Carl Greenleaf (who had purchased the Conn company from its founder) was a key figure in the founding of the "school band movement," transferring bands from their association with manufacturing concerns and local townships to school systems, thereby ultimately revivifying the musical instrument business.

Other factors were at work as well. The valved trumpet, which had been around about as long as the original cornets, had never gained wide usage. Valved trumpets in symphony orchestras were almost invariably pitched in low F or Eb, whereas cornets were commonly used for the higher-

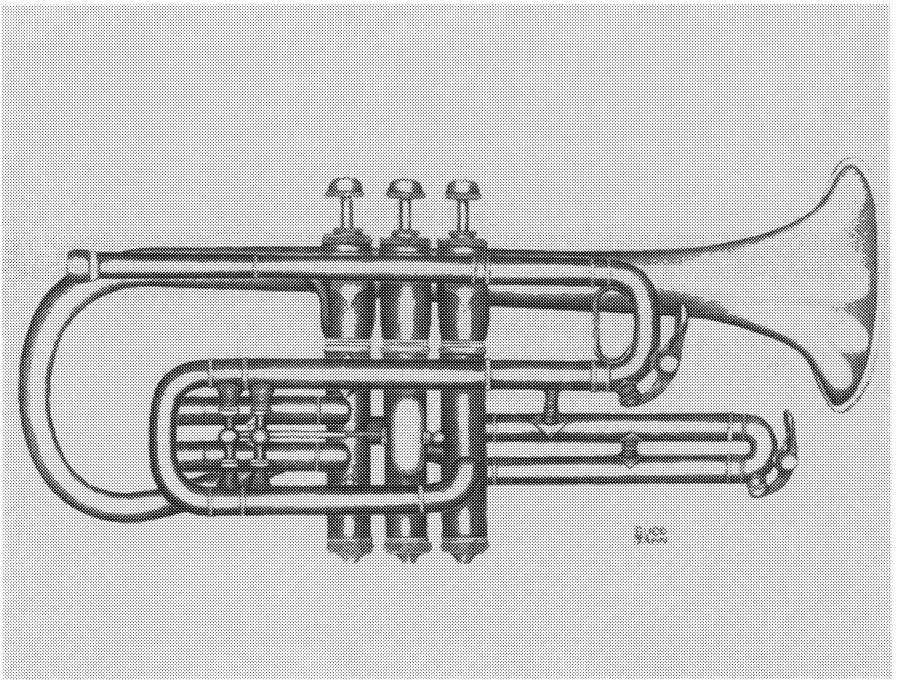


Figure 7. A Conn Perfected Wonder (cf. Figure 6). The S-shape configuration and longer bell hint at a more trumpet-like design. It is not yet certain whether Conn, or the rival Buescher Co. (Gus Buescher was a former Conn employee; both firms were in Elkhart, Indiana), or another, European firm, initiated this design. Total length: 14 1/2″. Drawing based on Conn 91660 (ca. 1905) in the author's collection.

pitched C-Bb and A soprano voicings. The modern Bb trumpet, apparently invented by the French Besson company in the mid-1880s (see Baines, 1992, p. 345; Eldredge, unpublished ms. A), was always a rare commodity.[18] Soon after World War I, however, valved Bb trumpets (often with rotary valves or other devices to allow a quick pitch change to A) began to appear in numbers. The great symbolic event was Louis Armstrong's dropping the cornet for a Bb trumpet around 1923 or 1924, supposedly after hearing dance band players using trumpets with great precision and projection on his first visit to New York.

[18] According to White (1980), the modern Bb trumpet was designed by the Belgian maker Victor Mahillon, acting as a consultant for the Besson firm in Paris in the 1880s (see also Baines, 1992, p. 345). I have been able to locate only four Besson Bb trumpets made prior to 1900, and fewer than a dozen made prior to World War I.

The historical pattern of valved trumpets, in the background for nearly a century, all of a sudden jumping to the fore and "radiating" into a diversity of styles and usages with the cornets simultaneously disappearing, strongly reminds one of the situation between mammals and dinosaurs. Dinosaurs became extinct not because of the mammals, but because of some ecosystem collapse (occasioned, apparently, by the impact of one or more comets). It was the demise of the dinosaurs that enabled mammals, finally, to radiate and take up the roles formerly played by dinosaurs in terrestrial ecosystems. In the case of cornets and trumpets, the triggering event seems simply to have been a human preference switch: 'twas humans, not trumpets, that nearly killed off the cornet.

Whatever the exact sequence of events and their underlying causes, by the mid-twenties almost everyone was playing trumpets—in symphony orchestras, on Broadway, in jazz bands and high schools. The 1923 Sears Roebuck catalogue offered no trumpets for sale; they were there, though, in 1924. The change happened nearly overnight, and cornets quickly fell into a major eclipse. Perhaps the only major exception to this generalization was in the British Brass Band tradition, where traditional cornets (in high Eb and Bb) continued to be played, manufactured by such companies as English Besson (later bought by Boosey and Hawkes) and the Salvation Army.

To be sure, Conn continued to make its model 80A, an unusual long bell cornet with a microtuning crook on the bell, a model that stayed in production well into the 1950s. The H. N. White Co., makers of "King" instruments, likewise continued to sell their equally uniquely-designed "Master Model" (a design preceding World War I). And Vincent Bach and many other makers began selling a non-shepherd's crook, fixed leadpipe, longbell version of the good old Besson Concertiste[19] in the mid-1920s, the cornet that continues to be the most prevalent design right up to the present day. For a time (1920s and 1930s), other makers sold cornets that looked more and more like trumpets—culminating in several models produced by Conn that were configured exactly like one of their trumpet models, but took a cornet mouthpiece and were advertised as cornets![20] Needless to say, the sudden near-extinction of cornets, fueled by the sudden efflorescence of

[19] Indeed, Bach, who was a professional soloist, brought his Besson Concertiste (serial no. 79696) with him when he immigrated to the United States in 1914 (see Smith, 1995, p. 21; Smith illustrates Bach's Besson cornet in his Figure 11, p. 12). The Besson valve porting system, originally exemplified in the older Concertiste and Desideratum models of the 1870s, were modified into their final form in the Concertiste model of 1888, and emulated by Bach. The Concertiste valve cluster has long since become the standardized configuration on trumpets and cornets throughout the industry.

[20] For example, the 40A and 40B rimless bell instruments of the late 1930s and early 1940s, and the later "Connstellations" of the 1950s.

trumpets, drastically curtailed the diversity of cornets so typical of the first two decades of the twentieth century.

5.5. 1985 Onwards. Nostalgia

A wave of nostalgia has gripped the brasswind world, and virtually all major manufacturers make a shepherd's crook model—albeit all with fixed leadpipes. Most of these resemble the Besson Concertiste (Figure 1), though some have the Courtois droop (albeit none with a double water key). In addition, some makers have actually designed new cornets models: for example, David G. Monette designed a cornet in C, and a similar one in Bb, that lack the characteristic extra 360° turn to the leadpipe (though Monette himself once again is offering a classic, shepherd's crook Concertiste model!).

Such episodes of rapid turnover (disappearance of long-stable older models, and sudden appearance of radically new designs) do bear close resemblance to the critical "threshold level" (turnover pulse/coordinated stasis) in the history of life, although in material cultural evolution theft of idea adds even greater complexity to the patterns of stasis and rapid diversification. Besides, the economic events that end one phase and usher in another seem to have as much to do with questions of style (what is thought appropriate for an age) as with critical factors (such as the highly dubious possibility that trumpets, rather than cornets, were better for use in radio broadcasts and recordings). The tendency to go towards longer-bell models in the 1900–1920 period, if anything, presaged the switch to the longer, sleeker trumpets.

6. CONCLUSION

Material cultural information, like genetic information, is manifestly hierarchically structured—a simple consequence of having had a history. However, given the nature of its transmission, material cultural information is almost invariably structured into more than one hierarchy. Both forms of information, taken alone, are static systems. "Evolution" (change in heritable information) comes only through interaction with hierarchically structured economic systems. Natural selection and cultural selection are the paradigmatic, base-level models, respectively, for such interactions.

But processes of selection do not provide the sole nexus for such a connection; neither do they provide the only mechanism for the generation of stasis and change in biological or material cultural systems. The history

of any subset of transmissible information must be examined in conjunction with the histories of economic systems, which are by definition cross-genealogical. Both biological and material cultural systems show patterns of economic, system-wide stability—meaning, as well, great stability in subsets of either genetic or material cultural information. These stable systems, however, are periodically interrupted by external events, prompting the extinction of some sets of information (biological taxa, cornet designs, still larger "families" of instruments), and the subsequent proliferation, in separate lineages, of novel taxa.

Evolution doesn't happen in a vacuum. Both material cultural and genetic information systems tend to remain stable unless or until they are either (1) driven to extinction, or, through the extinction of collateral lines, (2) stimulated to change rapidly. Although the patterns of historical development ("evolution") of both genetic and material cultural information are intriguingly similar, the details of causality underlying those patterns differ—in large part through the different nature of inheritance between these two classes of information—and in part because of the differences between biological and specifically human economic systems.

ACKNOWLEDGMENTS

I thank Nick Thompson for asking me to contribute to this volume of *Perspectives in Ethology*, and for his many wise and valuable comments. François Tonneau improved the manuscript mightily with his diligent editorial input. I also thank, for their insights and feedback, my colleagues at the American Museum of Natural History Robert L. Carneiro (ethnology) and Charles Spencer (archeology).

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Chapter 6

PITFALLS OF BEHAVIORAL SELECTIONISM

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ABSTRACT

Numerous analogies have been offered to relate evolutionary and behavioral phenomena. B. F. Skinner (1981/1988), in particular, has suggested that similar processes of selection operate at the levels of evolution, behavior, and culture. This essay examines Skinner's proposed analogy between natural selection and operant reinforcement. We argue that the analogy fails to characterize a shared causal structure. Operant reinforcement mimics superficial aspects of natural selection through entirely different mechanisms; hence no detailed understanding of operant behavior can be expected from selectionist notions. Selection analogies with respect to reinforced behavior are generally useless and probably misleading. The failure of Skinner's selection metaphor reflects on the current relations of some parts of psychology to evolutionary theory.

Perspectives in Ethology, Volume 13: Evolution, Culture, and Behavior
edited by Tonneau and Thompson, Kluwer Academic/Plenum Publishers, New York, 2000

1. OPERANT BEHAVIOR AND SELECTION

In 1938 B. F. Skinner published the first book-length treatment of his research on how consequences affect behavior. His experimental subjects were rats (*Rattus norvegicus*), the bit of behavior he studied consisted in lever pressing, and food was the consequence used to increase or maintain ongoing behavior (Skinner, 1938). Whereas previous research on similar issues had relied on discrete trials and complex acts organized in space and time, Skinner's studies (1938) made heavy use of an important innovation. In his new operant paradigm, the relevant behavior was in principle free to recur at any point in time, did not require extensive displacement of the subject's body, and consisted in a bit of behavior sufficiently short to be considered instantaneous. Considering lever pressing as an instantaneous event allowed the analysis to focus on the rate of behavior and how it changed over time, whereas previous research carried out with mazes or puzzle boxes often used latencies or completion times as dependent variables.

Figure 1 presents Skinner's basic findings in an idealized way, time flowing from left to right. A food-deprived rat, previously trained to eat from a food dispenser, was placed into the experimental chamber, which included a lever connected to the dispenser. While exploring the chamber, the rat sooner or later came to depress the lever (Figure 1, line *a*, first vertical dash on the left), this first lever press being followed by food (black dot in Figure 1). As a consequence, the rate of lever pressing immediately increased (line *a*). In Skinner's language, the operant response of lever pressing had been *reinforced* by food. The term *operant* was coined to distinguish this kind of behavior, emitted as it were in the absence of any clearly identifiable stimulus, and reinforceable by its consequences, from the reflexive or *respondent* behaviors that Pavlov had previously studied (1927) and that did involve an antecedent stimulus.

The increase in response rate obtained with operant reinforcement was typically instantaneous; contrary to common belief, response rate in Skinner's paradigm did not require numerous response-food pairings to reach an asymptotic level (line *a*). Plotted as a function of time, the local rate of lever pressing would typically jump to its maximal level after a single response-food pairing (line *b*). On the other hand, once the response had been reinforced, disabling the dispenser so that lever pressing did not result in food anymore often produced a gradual return to a lower level of responding. (How and why response rate decreases during this extinction procedure is actually a complicated issue, still the focus of much debate.)

In a clever experiment, Skinner (1938) strung reinforcement and extinction together to document how a single reinforcement could affect

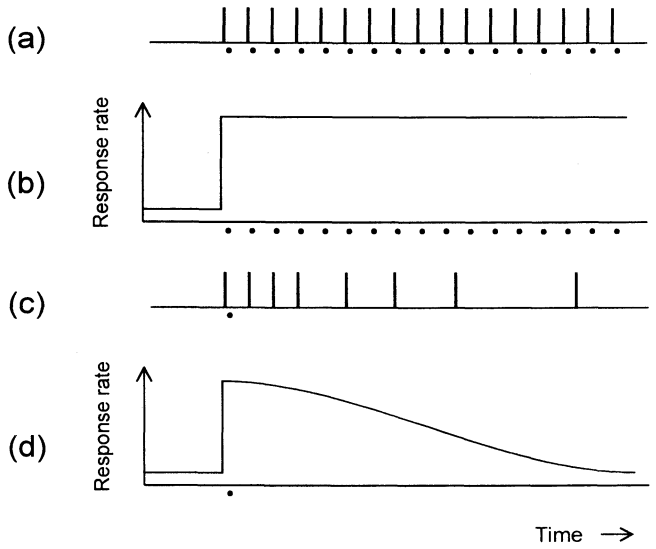

Figure 1. Some basic facts about operant reinforcement. Line *a*: Delivering food (black dots) after each lever press (vertical dashes) immediately increases the rate of lever pressing. Line *b*: How local response rate varies along line *a*. A single response-food pairing suffices to bring response rate up to its maximal level. Line *c*: If only the first response is reinforced, response rate increases as usual and then slowly reverts to its previous level. Line *d*: How local response rate varies along line *c*. Skinner's findings have been idealized to highlight the basic features of operant reinforcement.

the time course of operant behavior. He reinforced the first lever press and then immediately turned off the food dispenser. Response rate increased as expected after the response-food pairing and decreased gradually thereafter (Figure 1, lines *c* and *d*). Combining reinforcement and extinction episodes over time defines the field of operant schedules, which produce regular but complex behavior patterns (Iversen & Lattal, 1991).

1.1. Development of an Analogy

Skinner's 1938 work contained no hint at a possible analogy between operant reinforcement and natural selection, although metaphorical, selectionist treatments of learning, thinking, and other psychological phenomena had existed in the literature since the nineteenth century (see reviews in Campbell, 1960, 1974; Plotkin, 1987). Skinner's later book, *Science and*

Human Behavior (1953), aimed at a more general psychological audience, contained only a few allusions to a possible analogy between operant reinforcement and natural selection. On page 90 he wrote: "In both operant conditioning and the evolutionary selection of behavioral characteristics, consequences alter future probability." And later: "In certain respects operant reinforcement resembles the natural selection of evolutionary theory" (1953, p. 430). Skinner also shortly mentioned a similar selection process in cultural change (p. 434).

Skinner's writings on such analogies became more frequent in the following decades (Plotkin, 1987, provides a detailed chronology), to culminate in an article entitled *Selection by Consequences* first published in *Science* in 1981. The core of Skinner's proposal was that a similar mechanism of selection, conceived as a particular "causal mode" (1981/1988, p. 15), operates in a parallel fashion at the levels of evolution, behavior, and culture. Natural selection is a type of "selection by consequences" (p. 11) that made its appearance with the first self-replicating molecules (p. 11). The selection of behavior by its consequences, on the other hand, consists in operant reinforcement (pp. 12–13), a process whereby responses are strengthened by the events following them. Cultures also exemplify selection by consequences, and evolve when the practices originating within a group "contribute to the success of the practicing group in solving its problems" (p. 14). In Skinner's framework, a question raised at any one of the three levels must have parallels at the other two and calls for an answer in terms of variation and selection (p. 14), perhaps combined with "structural constraints" (p. 15). The only distinguishing features of operant reinforcement mentioned in a section entitled *Similarities and differences* are the speed at which reinforcement proceeds (p. 14) and the fact that whereas biological traits and cultural practices are actually passed from one generation to the next, reinforced behavior is "transmitted" merely in the sense "of remaining part of the repertoire of the individual" (p. 15).

Judging from titles such as *The Selection of Behavior* (Catania & Harnad, 1988) and from the content of introductory textbooks written from a behavioral standpoint (e.g., Baum, 1994, p. 67; Catania, 1992, p. 38), Skinner's selectionist analogy appears to have played a prominent role in behavior analysis. However, a close reading of the literature reveals that in fact Skinner's proposal has not fostered any research program that could substantiate the analogy at a behavioral level (Plotkin, 1987). The use of the selection analogy in behavior analysis often amounts to nothing more than a restatement of its general theme, sometimes compounded with the further claim that the "selection" of behavior by its consequences is simply a "fact" established beyond dispute (Chiesa, 1992, p. 1291).

A wholly metaphorical language reminiscent of (some aspects of) evolutionary biology is thus imposed on data that have actually been

gathered, and interpreted, without any inspiration from the selection metaphor. If no trace of selectionism can be found in Skinner's early work, more recent developments in operant research (e.g., Davison & McCarthy, 1988) bear no trace of selectionism either (the few exceptions to this trend will be discussed below). How irrelevant Skinner's selection metaphor can be to real operant research may perhaps be most easily understood by considering McDowell and Kessel's (1979) linear-system model of reinforcement. This model simply assumes that operant behavior is driven by reinforcement inputs (see McDowell, Bass, & Kessel, 1983, p. 165) and that the resulting input-output relations can be described by a transfer function. All of the predictions of the model derive from this single hypothesis. No mention is ever made of "variation" and "selection." The selection metaphor seems even more foreign to the work of behavior analysts who study the modulation of operant performance by stimuli and antecedent operations (e.g., Michael, 1993). Consequently, even some proponents of Skinner's views have recently admitted that "although *selectionist* is an adjective often applied to the behavior-analytic paradigm, the serious work of explicating what that means has barely begun" (Glenn & Madden, 1995, p. 249, italics theirs).

1.2. Psychology in Disarray

Why has the "serious work" of explicating behavioral selectionism barely begun? Could more work along these lines eventually prove fruitful and suggest some "underlying identity of process" (Plotkin, 1987, p. 142) between operant reinforcement and natural selection? Or, alternatively, could Skinner's selectionist view of behavior prove so superficial as to remain useless if not downright misleading? The question, we believe, is significant for three reasons that extend far beyond the confines of contemporary behavior analysis.

Firstly, psychology as a whole has often been portrayed, with some justification, as a confusing patchwork of inconsistent and arbitrary explanatory attempts (e.g., Tooby & Cosmides, 1992, p. 23). Relating psychology to evolutionary biology might well impose some order on this patchwork and diminish the arbitrarity of psychological principles by grounding them in independent evidence and theory (see Barkow, Cosmides, & Tooby, 1992). However, the proposed bringing together could in principle take two paths. A first, "vertical" approach would be to focus on causal dependencies among behavioral and evolutionary processes. The resulting framework should presumably describe complex feedback relations within a hierarchy of behavioral, ecological, and evolutionary levels (cf. Lewontin, 1983; Odling-Smee, Laland, & Feldman, this volume). The

second, "horizontal" approach would be to look not for causal relations but for analogies among levels, in the hope that such analogies reveal an underlying commonality of process. Skinner's (1981/1988) suggestion that similar mechanisms of selection operate in evolution and behavior clearly belongs to the second class of integrative proposals. Assessing the adequacy of Skinner's selectionist claims about behavior could have suggestive implications for the respective merits of vertical and horizontal approaches.

Secondly, the notion of operant reinforcement as a process of selection has been apparently accepted at face value by the major proponents of a sweeping selectionism extending largely beyond evolutionary biology (see Campbell, 1960, 1974; Cziko, 1995, ch. 7; Dennett, 1995, pp. 374–375; Plotkin, 1987). Showing that the notion of operant selection fails theoretically and empirically could reflect centrally on such views. At the very least, the failure of operant selectionism would suggest caution before accepting a notion of selection sufficiently "substrate-neutral" (cf. Dennett, 1995, p. 82) to have significant implications outside of evolutionary biology, especially when this "neutrality of substrate" is illustrated by reference to reinforcement (e.g., Cziko, 1995).

Finally, the contrast between Skinner's selectionist language (1981/1988) and its general lack of empirical accomplishments confirms the recent suspicion that appeals to evolutionary theory in psychology are not always free of rhetorical motives (see Lloyd, 1999). Most strikingly, while various research programs in psychology all claim some support from evolutionary biology (e.g., Tooby & Cosmides, 1992; Donahoe & Palmer, 1994; Piattelli-Palmarini, 1989), the very same process of operant reinforcement can be presented either as selection (Donahoe & Palmer, 1994, p. 37) or as its exact opposite (Piattelli-Palmarini, 1989, p. 29, p. 35), depending on the author's allegiance. Making sense of such conflicting claims calls for a more detailed analysis of how evolutionary analogies in psychology actually relate to natural selection.

1.3. Correspondence of Components

Any pair of phenomena taken at random will exhibit shared as well as unshared features. In the analogy between reinforcement and natural selection, as in other analogies, central features must be identified and irrelevant ones left aside; looking for a close analog of haplodiploidy in operant behavior would presumably be a waste of time. On the other hand, the central features of the analogy should be indicative of a shared causal structure (Darden & Cain, 1989). Without detailed implications for causal processes, a purely formal analogy is vacuous. Thus the human face has seven holes, and seven is also the number of days in the week; but nothing follows from this exercise in numerology. Finally, using a metaphorical

model adequately should entail specifying exactly what corresponds to what in the two domains being compared. In the absence of such specifications, how a mere metaphor could contribute to our understanding remains unclear.

A main problem with the putative analogy between operant reinforcement and natural selection, however, is that once a few components of the analogy (such as variation and selection) have been mentioned, the correspondance of parts is rarely, if ever, ascertained. Yet natural selection necessitates a very precise arrangement of components (Endler, 1986; Williams, 1966).

Skinner's (1981/1988) phrase of "selection by consequences" is a good case in point. Talking of consequences seems to identify an obvious commonality of operant reinforcement and natural selection. Yet further reflection reveals suspicious features. In operant reinforcement, consequences like food or water are actually delivered in the *environment*. Construing such events as agents of selection easily follows from the behaviorist emphasis on the environment as a primary factor of behavioral change (see Figure 1), combined with a selectionist approach. Now consider a simple case of natural selection: Antibiotic is sprayed on two genetically different strains of bacteria. As a result, only one strain survives. Where is the "consequence"? Definitely not in the environment. Spraying the antibiotic cannot be a consequence of anything because antibiotic was sprayed on *both* strains of bacteria. The only "consequence" we can think of in this example resides not in the environment but in the *organism* and consists of dying. More generally, in mortality selection the agent that has consequences for reproductive success is not itself a consequence but rather a common ecological challenge (cf. Freeman & Herron, 1998, pp. 267–291). Yet mortality selection is indisputably a case of natural selection (Endler, 1986).

This kind of discrepancy suggests that even though operant reinforcement and natural selection may both involve feedback, the underlying relations are probably arranged quite differently. Evaluating a putative correspondence between operant reinforcement and natural selection thus cannot proceed without an analysis of natural selection part by part. This analysis should move beyond generalities by detailing, not only what natural selection is, but also what it excludes. This second point has often been neglected in evolutionary analogies.

2. SELECTION PROCESSES

Any instance of natural selection must take place in a population whose members differ among themselves in some trait(s). To simplify the argument we focus on a single phenotypic trait with two discrete values A

and B, so that all members of the population are either of the A or of the B type. A phenotypic formulation of natural selection (see Endler, 1986, p. 4) is preferable for a fair assessment of Skinner's analogy, which was developed at a purely behavioral level; properties of the genetic system will nevertheless be discussed when necessary, capitalizing on the useful fiction of a one-to-one mapping from genotypes to phenotypes.

To ascertain changes in the composition of the population, we need some criterion to identify what constitutes the "same" population across time (see Darden & Cain, 1989). We also need a criterion to include in the same population individuals that differ among themselves. The most relevant criterion, chosen to guarantee some causal homogeneity to the dynamics of a possible selection process, consists in a common environment or set of ecological conditions (for more discussion see Brandon, 1990; Damuth, 1985). Thus, lumping in a single "population" two distant groups encountering radically different ecological challenges, and evolving in entirely independent ways, would be useless from an explanatory perspective even though mathematically feasible (Damuth, 1985, p. 1134; Sober & Lewontin, 1982, p. 170).

2.1. Selection Implies Sorting

Evolution by natural selection implies a change in the numerical composition of the population being considered, but not any change will qualify. At the very least, the change in proportion of A and B individuals should be a case of *sorting* (Vrba & Gould, 1986), that is, of differential death or reproduction among A and B individuals. A population can evolve though other means than sorting. Mutations and migrations, for instance, do not demonstrate sorting because they involve neither death nor reproduction of different individuals.

Sorting can be accomplished in two different ways, by simple mortality (Figure 2, panel *a*) or through differential reproduction (Figure 2, panel *b*). In Figure 2a, the population before sorting includes an equal number of A and B members. Whereas the B members remain alive (or maintain their structure), the A members die (or collapse). The composition of the population therefore changes: from a population including both A and B members to a population including B individuals only. This type of sorting requires no reproduction mechanism passing structure from one individual to another, but merely the differential stability of phenotypes through time (cf. de Duve, 1987). Note that this type of sorting cannot by itself increase the absolute number of either A or B individuals. However, if some background mechanism continuously produces A or B individuals at random, B individuals will eventually accumulate in the environment.

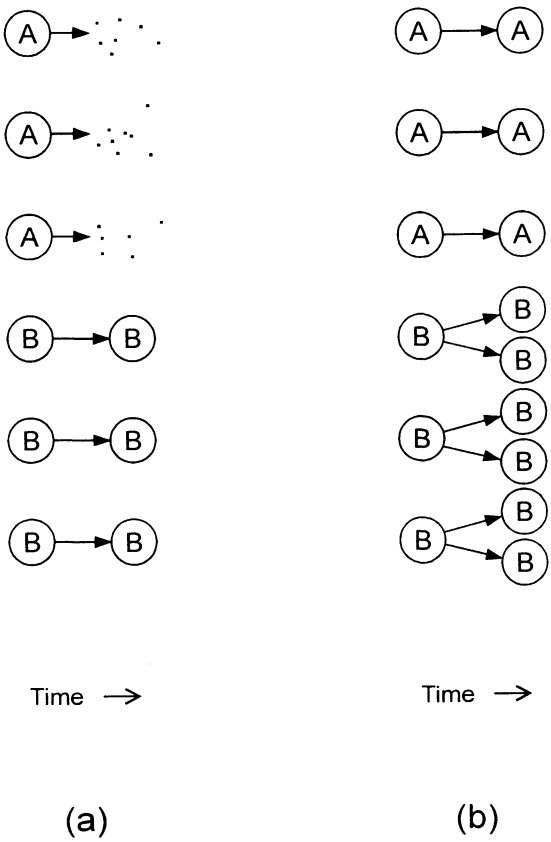

Figure 2. Two types of sorting. Panel *a*: Sorting by mortality. Whereas the B individuals remain alive, the A individuals die. The horizontal arrows indicate permanence of structure instead of actual reproduction. Panel *b*: Sorting by differential reproduction. The A and B individuals reproduce at different rates, the A versus B difference showing inheritance. Here the horizontal arrows represent actual reproductive relations.

Figure 2b exemplifies sorting through differential reproduction. Starting from a mixed population of A and B members, B individuals reproduce at a higher rate than A individuals do. If the A versus B difference shows inheritance, that is, if it tends to be conserved through reproduction, the composition of the population will shift toward a higher proportion of B individuals (as in Figure 2a, but for different reasons).

Sorting through differential reproduction (Figure 2b) brings us quite close to the classic definition of natural selection as a process combining variation with inheritance and differential reproductive rates (e.g., Lewontin, 1970), although one condition is still missing to obtain full-fledged

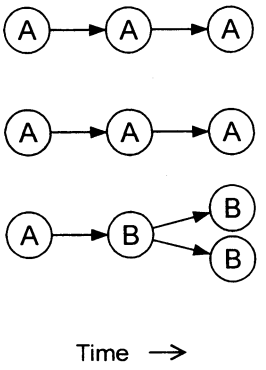

Figure 3. Two steps in Darwinian evolution. The first step implies mutation (or any other source of genetic novelty). Note that mutation is not sorting: Even though the composition of the population changes, this change of composition does not arise from differential death or reproduction. Once variation across individuals is available, however, the second step of Darwinian evolution can proceed. This second step consists in sorting, here exemplified by differential reproduction. (For simplicity we neglect the step of development; see Gilbert, Opitz, & Raff, 1996.)

natural selection (see below). A clear focus on sorting allows a better understanding of Darwinian evolution through natural selection, which comprises the origin of variants as well as their spread in the population (Endler, 1986, p. 7, p. 51). The first step in Darwinian evolution, the origin of variants, is not a case of sorting but a process of mutation. (For simplicity we neglect all other sources of genetic novelty such as recombination). The second step of Darwinian evolution, phenotypic selection (sometimes called simply "selection:" e.g., Wade & Kalisz, 1990), *is* a case of sorting however (Figure 3).

The distinction between these two steps is fundamental to modern evolutionary theory, which assumes Darwinian evolution by natural selection, rather than Lamarck-type mechanisms (Futuyma, 1998; Mayr, 1982). Evolution by natural selection requires two steps precisely because variation (the first step) is effectively decoupled from adaptation, which results from sorting (see Sniegowski & Lenski, 1995). If variation *were* always adaptive, no further step would be necessary; variation alone would suffice.

Note, however, that the ability to demarcate variation (the first step) from sorting or phenotypic selection (the second step) in turn implies the ability to discern mortality from mutation, and reproduction from failure to mutate. If these distinctions cannot be made, the very idea of evolution by natural selection (Figure 3) collapses.

2.2. Implications for Temporal Change

Distinguishing mutation from sorting implies that the temporal changes of a single system cannot normally feed into a selection process. A selection process requires spatial variation across different individuals, as opposed to *temporal* variation in a single individual. For the sake of the

argument, imagine an individual (thing, system) passing through the successive states A, B, C, D to later stay in state D. One might be tempted to describe the A → B → C → D changes as "variation," and the later permanence of D as a step of "selection." But the "variation" here cannot be distinguished from mortality, nor "selection" from failure to mutate. Does the A → B transition, for instance, document the death of A immediately followed by the birth of B, or just a mutation from A to B? Does the persistence of D document its "staying alive" or its failure to vary?

This logical problem raises serious doubts about selectionist analogies that treat purely temporal change as "variation" (e.g., Campbell, 1956; Skinner, 1981/1988). Although such analogies nominally appeal to the couple of variation and (phenotypic) selection, they may not allow any actual distinction between variation and sorting. Now in evolution by natural selection, mutations also occur across time in individual lineages. But this temporal variation will be acted upon by sorting only after being converted into spatial, across-member variation through the branching process of reproduction. That developmental (Sober, 1984, pp. 147–155) or transformational (Futuyma, 1998, pp. 21–22) evolution could in principle take place in a single lineage, whereas evolution by natural selection cannot, is presumably no accident.

A related concern is that repetition over time does not imply reproduction. In Darwinian evolution, individuals that multiply through reproduction accumulate in space as well as in time. Branching actually entails the availability of individuals for further sorting. But how reproduction could occur in the temporal domain of a single individual is unclear. On the other hand, the successive transformations of a single system easily generate recurring events. When a heated neuron increases its rate of firing, for example, its spikes repeat but do not reproduce: Spikes do not play any positive causal role in bringing out later spikes, as should be the case if firing involved reproduction. Temporary events like spikes, that repeat but neither persist nor reproduce, cannot be submitted to sorting.

2.3. Selective Processes Versus Processes of Selection

Even when the processes dubbed "selective" in some evolutionary analogy or another properly involve variation across individuals, these processes rarely qualify as sorting. Selectionist metaphors frequently fail to distinguish processes that are merely selective from processes of selection. A *selective* process is just any process that affects an individual rather than another. A process of *selection*, however, must at the very least involve sorting, that is, mortality or reproduction (Vrba & Gould, 1986). An obvious difficulty with the notion of selective process is that almost any physical

process may be construed as selective, contradicting the more technical concept of selection. Imagine three buckets for example, all of them empty. Someone fills one of the buckets up to the top. The filling is selective: It affects one bucket rather than the others. No sorting is involved, however. No bucket died, no bucket lost its structure, no bucket multiplied.

Failing to demarcate selective processes ("selection" in the colloquial sense) from processes of selection (in the technical sense implying sorting) would turn evolutionary theory into nonsense. Within an evolutionary context, *migration* can certainly be a selective process. Some individuals may migrate whereas others stay in the population (defined by geographical and ecological boundaries). Yet migration is not selection (Falconer & Mackay, 1996, ch. 2). Worse, *mutation* can also be a selective process. Imagine a population of two members where a mutation arises, but only in one individual. The mutation is by definition *selective* since it affects one individual rather than the other. But does this mutation exemplify *selection*? Obviously not (Falconer & Mackay, 1996, ch. 2). Another case of selective mutation might involve two strains of bacteria, only one of them exposed to a mutagen such as caffein. Because of the mutagen, mutation rates will probably be higher in one strain than in the other. Exposing only one strain to the mutagen is thus a *selective* process, though not a process of selection. (Of course, mutants may be exposed to phenotypic selection, hence sorting. But mutation itself cannot exemplify selection.)

A focus on sorting suggests some caution before adopting Jerne's well-known distinction (1967) between instructive and selective processes, a distinction on which some selectionist analogies rely heavily (e.g., Cziko, 1995; Piattelli-Palmarini, 1989). This distinction originates in the context of immunology. Jerne (1967) defines selection as any "mechanism in which the product under consideration is already present" (p. 205) before the arrival of a "signal" and is thereafter "recognized and amplified." However, any system in which the amplification happens must be "capable of receiving a signal" and is therefore "subject to instruction by this signal" (p. 205). Jerne's distinction between instruction and selection is thus one of level: What appears as "instruction" at the level of a whole system may actually involve "selection" at the level of its building blocks (pp. 203–205).

One case mentioned by Jerne (1967) involves the translation of messenger RNA in proteins. This process is said to involve selection at the level of individual transfer RNAs (if not of the proteins themselves) on the ground that the messenger RNA must "select" among a pool of available subunits (p. 204). Yet the selective choice of transfer RNAs implies no more sorting than the choice of a bucket to fill it with water. The proposed example of selection does not even seem to fit Jerne's (1967) requirement that selection should involve the amplication of a preexisting product. In the recognition of transfer RNAs no "product" (transfer RNA) is

"amplified." Again, a process that is merely selective has been confused with a process of selection. On the other hand, Jerne's explicit definition of selection (p. 205), once restricted to amplification through differential reproduction, may correctly imply sorting. In any case, some selective processes apparently involve neither "instruction" nor sorting.

Finally, dubbing "selection" any interaction whereby a complex system takes one path rather than another, on the ground that the environment must have "selected" one course of action over the others, bears no coherent relation to the concept of selection in evolutionary biology. On this ground, any putative case of *mutation* induced by the environment (see Lenski & Mittler, 1993; Thaler, 1994) would necessarily count as "selection." But sorting can operate only on concrete individuals (Hull, 1980) and not on possible courses of actions or other potentialities.

2.4. Selection and Drift

Although natural selection entails sorting (differential death or reproduction), not all cases of sorting constitute natural selection (Vrba & Gould, 1986). A last condition must hold. The sorting process must involve heritable differences and be actually influenced by one or another of the heritable differences being sorted. If various heritable differences are being sorted simultaneously, an influence of all of them is not actually required; a heritable difference that does not influence sorting may well be selected through its correlation with another heritable difference that does (cf. the distinction between "selection of" and "selection for" in Sober, 1984). But the causal influence of *at least one* heritable difference is needed to exemplify natural selection. Sorting processes that take place irrespectively of *any* heritable difference do not exemplify natural selection. They are normally classified as drift (see Hodge, 1987; cf. Beatty, 1984, 1992).

Imagine a population of birds with red and green individuals, for instance. The red birds are less cryptic and predation affects them disproportionately: As a result, the proportion of green birds in the population increases. Because sorting is influenced causally by a heritable difference (being green versus being red), this example qualifies as natural selection. A causal relation *actually holds* between the heritable difference in color and differential predation. Now imagine another population of green and red birds. A forest fire destroys an area of the birds' habitat where, "by chance," (read: for reasons independent of any heritable difference) red birds happen to be more numerous. As a result, the proportion of green birds in the population increases. In this case differential mortality, or sorting, is independent of any heritable difference. No causal relation actually holds between the difference in color, or indeed any other heritable

difference, and the fact that the red birds are differentially exposed to the fire and die. In this case, therefore, the observed sorting cannot qualify as natural selection.

A common mistake, encouraged by the careless use of the notion of "chance," is to believe that drift is somehow uncaused or that any difference among the individuals being sorted is irrelevant to it. Further reflection shows that drift is no less a causal process than natural selection (Hodge, 1987) and that some differences among individuals are relevant to it; but these differences are not heritable. In drift the differences that govern the course of sorting involve temporary, non heritable temporal and spatial relations. In the example of the fire, what causes the red birds to die disproportionately is a physical property of these birds: their physical property of being in the zone, call it X, where fire strikes. The (physical) difference between occupying and not occupying X presumably shows no inheritance, however; hence the observed sorting cannot exemplify natural selection.

Other phenomena usually classified as drift, such as the founder effect (Falconer & Mackay, 1996, p. 78; Futuyma, 1998, p. 304; Hartl & Clark, 1997, p. 291), document a similar involvement of non heritable, spatio-temporal differences in the causation of sorting. Brandon (1990, p. 46) thus discusses the example of two genetically different types of seeds, *a* and *b*, dispersed by the wind over a patchy field of fertile and toxic soils. "By chance" (read: for reasons entirely independent of their genotype) a disproportionate number of *a*'s land in fertile soil, so that the proportion of *a*'s in the field as a whole increases. This change of proportion exemplifies sorting but not natural selection: Differential reproduction affects the proportion of *a* and *b* seeds, but is not itself affected by the *a* versus *b* difference, nor indeed any other heritable difference.

Of course, if some seeds inherited a mechanism for influencing where to land, and if having this mechanism entailed a higher reproductive success, a causal relation from heritable variation to sorting would be restored, and sorting would document natural selection (on habitat choice). In the absence of such a causal relation, however, any observed sorting tells us more on the heterogeneity of the environment than on the properties of the individuals being sorted (Brandon, 1990, p. 46). Again, consider two genetically different strains of bacteria, only one of them being sprayed ("by chance") with an antibiotic. The fact that the bacteria in one strain die more than in the other cannot be attributed to natural selection. From the viewpoint of natural selection, the mortality rates in the two strains cannot even be meaningfully compared, the observed sorting resulting directly from the heterogeneity of the environment (antibiotic versus no antibiotic) rather than from any heritable difference among the strains. One strain does worse than the other not because of its genetic composition interacting with the

environment, but simply because of a spatial coincidence with the antibiotic. Had the other strain been at the same place and at the same time, it might have suffered equally.

In sum, natural selection is a process where at least one heritable difference among the members of a population causally influences the sorting of these members (see Hodge, 1987). How sorting proceeds can in principle be studied by counting the individuals of different types. Once the properties of inheritance and sorting (differential reproduction or mortality) have been worked out, the composition of the population changes according to the laws of "probability" (Endler, 1986, p. 5) or better, arithmetic (counting). Counting can of course raise difficulties of its own (Janzen, 1977); but the very existence of such problems suggests that the individuals actually submitted to sorting have not been properly identified (cf. Buss, 1983). An added complication is that sorting can take place at different levels simultaneously (Lewontin, 1970; Sober, 1984; Vrba & Eldredge, 1984). Sorting leads to evolution unless counteracting factors, such as a bias in the inheritance system, intervene.

Although the present definition has been set in a biological context, it generalizes easily to any population of entities exhibiting heritable variation and submitted to sorting. Thus our sketch does not necessitate any mention of genes, cells, or organisms (cf. Lewontin, 1970). We stress, however, that some criteria distinguishing death (or loss of structure) from mutation, and reproduction from failure to mutate, must be available; otherwise the very idea of evolution by natural selection, relying as it does on the two logically distinct steps of variation and sorting, collapses.

3. EVALUATING SKINNER'S SELECTION ANALOGY

Were Skinner's selectionist metaphor (1981/1988) basically correct, operant behavior should exhibit features analogous to heritable variation and sorting. In fact Skinner's metaphor fails on both counts. Consider the putative "variation" and "selection" of operant behavior, for example. In its initial explorations of the operant chamber, the rat's performance is undisputably variable. After the rat presses the lever for the first time, and after this first lever press is reinforced by food (as in Figure 1), behavioral variation immediately diminishes as the rat now spends most of its time pressing the lever and consuming food from the dispenser.

However, the "variation" of performance involves time, a fact that already raises grave doubts as to the validity of any analogy with natural selection. As the rat explores its environment, each of its moves involves a continuous reorganization of the whole body, a transition from one

configuration to another. In this continuous "stream" of behavior (Golani, 1992; Schoenfeld & Farmer, 1970), how can response mortality be distinguished from mutation? How does selection differ from failure to mutate? In the absence of empirical criteria for discerning the genealogical relations among responses, attributing a response change to sorting (granting that the concept makes sense in the temporal domain) rather than mutation or failure to mutate, seems highly arbitrary.

But let us waive such logical objections. Let us simply postulate with Skinner that any increase in the rate of a reinforced response results from the operant analog of sorting, free of any contribution from response mutation (cf. Staddon, 1977a). If this postulate is accepted, the increase of response rate through reinforcement should be analogous to a process of reproduction. However, the notion that responses reproduce seems to make little empirical sense. Even at a purely formal level the notion fails, as the existence of phenomena like discrimination proves (Timberlake, 1988). In discrimination training, a response (B) is reinforced in the presence of a stimulus E, for example, and never in its absence (see Catania, 1992, ch. 7). If all goes well responding will eventually occur only in the presence of E, and the experimenter will be able to turn responding on and off simply by manipulating the stimulus. However, that responses reappear when E is turned on, even though response rate was literally zero in the preceding time interval (in the absence of E), is inexplicable from the viewpoint of behavioral selectionism. Analogously, if an allele has been lost from the gene pool, selection cannot reintroduce it back: A frequency of zero cannot increase by reproduction. On the other hand, *mutation* could reintroduce the lost allele. The modulation of response rate by a stimulus E is thus analogous to directed mutation.

Countering that reinforcement "selects" entire relations between environment (E) and behavior (B), rather than mere responses (B), does not make the selectionist analogy any more defensible. Explaining in selectionist terms how a relation E → B (absent as it is when E is absent) can reappear on command in the presence of E is just as difficult as explaining how a mere response (B) could do so; unless the "relations" alluded to turned out to be "potential" relations, in which case the selectionist analogy violates the basic requirement that sorting can affect concrete individuals only.

3.1. Further Objections

Discrimination is not the only operant phenomenon where a response, apparently lost, can suddenly reappear when the environment changes (e.g., Brimer, 1972). The difficulties that such phenomena raise for

behavioral selectionism have been implicitly admitted by some of its advocates. Glenn and Field (1994), for example, have been led to distinguish the operant unit, a population spread across time and comprising various "instances of operant behavior" (p. 243), from these instances (the individual responses) themselves. Whereas selection properly applies to the operant unit, questions about its individual instances cannot be answered fully in selectionist terms. The occurrence of individual responses is rather explained by postulating an "instantiating function" of the environment (p. 252). In discrimination for example, selection would explain why responding persists at all at a global level, whereas the reappearance of responses when a stimulus E is turned on would result from E's "instantiating function."

Postulating such an "instantiating function" amounts to concede that responding is modulated locally in ways different from what a selectionist perspective allows. But once an "instantiating function" (analogous to directed mutation) has been added to the selectionist outlook, why postulate "selection" and an operant "unit" at all? Glenn and Field (1994) try to distinguish "the *existence* of operant *units*" from "the *occurrence* of operant instances" (p. 242, italics theirs), but what evidence is there for the "existence" of an operant unit, aside from the occurrence of the very instances that it is said to comprise? Glenn and Field's (1994) proposal that selection accounts for some "population characteristics" (p. 247) like the frequency of individual responses (p. 245) similarly fails. The frequency of responding averaged *across* stimuli (say, across E and non-E) can be manipulated at will merely by changing the frequency of the *stimuli* (E) evoking each response instance (B). Hence a frequency averaged across stimuli cannot serve as a valid index of "selection." The frequency of response *within* each stimulus condition (E), on the other hand, cannot be the result of a selection process either (see above); according to Glenn and Field it is the result of an "instantiation." Either way, selectionist analogies cannot cope with so basic a behavioral fact as discrimination (see Timberlake, 1988).

If behavioral selectionism fails in terms of variation and sorting, its supposed source of feedback, reinforcement, also proves problematic. The sharp increase in responding evident after a single response-food pairing (Figure 1) does not necessarily occur because of a causal relation actually holding between responding and food. The rat locked in the chamber has no actual contact with the reinforcement apparatus hidden behind the wall. Thus if food is dropped into the chamber wholly independently of responding, but happens "by chance" to follow a lever press with the same temporal and spatial relations as in Figure 1, line *c*, response rate must increase exactly as it does in Figure 1, line *c*; to believe otherwise is to credit the rat with extrasensorial perception. Of course, the long-term effects of presenting food independently of responding differ largely from those of

consistent reinforcement (for further analysis see Staddon, 1977b). These differences in the long term, however, must again involve purely spatial and temporal relations among responding and food, for these are the only relations exemplified inside the chamber (as opposed to the other side of the wall, where the programming apparatus resides).

The fact that a response can be reinforced entirely "by chance" (Henton & Iversen, 1978) suggests a last fundamental difference between natural selection and reinforcement. For natural selection, by definition and in contrast to drift, cannot be produced entirely "by chance." Granting the evolutionary analogy, the reinforcement of lever pressing through a temporal relation with food parallels Brandon's example (1990) of some seeds growing more quickly because of their purely spatial relation to a fertile patch. In both cases, the observed increase is caused not by any heritable difference (seed type *a* versus seed type *b*, pressing versus not pressing) but by some non heritable relation to the environment (a spatial relation in the case of the seeds, a temporal relation in the case of lever pressing).

Reinforcement is thus "superstitious in the most fundamental sense" (Donahoe, Crowley, Millard, & Stickney, 1982, p. 515). It takes place, not because a causal relation *actually holds* between the reinforced response and the reinforcing agent, or indeed between any response and the reinforcing agent, but because some response occurs in "a specified temporal relation" (Donahoe et al., 1982, p. 515) to this agent (as in Figure 1, line c). Natural selection is never superstitious in this sense, however (Endler, 1986). It takes place because a causal relation *actually holds* between at least one of the heritable differences being sorted and its fate in sorting. Hence even if operant reinforcement had an analog in evolutionary theory, this analog could not be natural selection but should include various forms of drift.

This last difficulty may not appear as damaging as the others we have reviewed: After all, both natural selection and drift exemplify sorting. But when all of the difficulties are pieced together, the resulting picture seems rather disheartening. Skinner's selectionist analogy fails in virtually all of its aspects. With or without amendments such as Glenn and Field's (1994) "instantiating function," the metaphor of selection cannot even address a phenomenon as basic and ubiquitous as stimulus discrimination. That Skinner's analogy requires ad hoc modifications even in its early stages of development is in itself quite revealing.

3.2. The Analogy at the Neural Level

Some advocates of behavioral selectionism have recently suggested that their program will better succeed if it includes neural as well as

behavioral elements. The suggestion is to develop separate analogs of replicators and interactors (Hull, 1980, 1981) instead of pursuing the selectionist program at a purely behavioral level. Accordingly, the operant responses observed in any reinforcement experiment are seen as *interactors* analogous to whole organisms, and their neural precursors as *replicators* analogous to genes (Donahoe, Burgos, & Palmer, 1993; Glenn & Madden, 1995).

Skinner's purely behavioral metaphor is also compared to evolutionary biology before the modern synthesis. According to Glenn and Madden (1995), for example, "if neural events are the behavioral units of replication," then standard behavior analysis is in much the same position as "evolutionary theory was before the rediscovery of Mendel" (p. 247). Adding neural replicators (p. 247) to operant interactors (p. 241) is supposed to complete the evolutionary metaphor and perhaps unleash its hidden explanatory power (also see Donahoe, Burgos, & Palmer, 1993, p. 19).

We are skeptical of this historical comparison and its supposed lessons. Darwin's ignorance of genetic mechanisms, although troublesome, did not prevent him from giving clear evidence of inheritance and sorting (e.g., Darwin, 1859, ch. 1) and from devising independent tests of his views (pp. 358–363 for instance). His theory of common descent also made sense of an enormous array of facts that had no explanation on competing accounts. By contrast, the identification of genealogical relations among reinforced responses seems to be purely definitional, a matter of free postulation. Yet, even this postulation of inheritance and selection in the abstract fails on simple grounds (see above).

Let us nevertheless grant operant selectionists their historical claims, and examine their approach to neural replication and behavioral interaction (Glenn & Madden, 1995). The most developed models in this "biobehavioral" approach to operant selection (Donahoe & Palmer, 1994) have the general outlook of the connectionist networks that have recently become popular in psychology (e.g., Rumelhart et al., 1986). A complicated net of input units, intermediary nodes, and response units is supposed to underlie the reinforcement process. Any presented stimulus (E) activates some input unit, the resulting activation tracing its way inside the network until some response (B) gets emitted as output. Operant reinforcement strengthens any active connection, so that the E $\rightarrow$ B relation most active at reinforcement time gets preferentially strengthened (see Donahoe, Burgos, & Palmer, 1993, Appendix, for more details). This kind of network can indeed simulate many aspects of reinforcement, extinction, and discrimination (Donahoe, Burgos, & Palmer, 1993; Donahoe & Palmer, 1994).

The simulations reported in the literature are certainly provocative; at the very least they demonstrate the heuristic value of modelling operant performance in terms of "selection networks" (the term chosen by Donahoe and colleagues to describe their connectionist models). But do these

accomplishments, impressive as they are, actually establish some parallel between reinforcement and natural selection? That connectionist networks can be made to simulate various aspects of behavior is well known, and the connectionist movement did not wait selection metaphors to proceed (e.g., Anderson, Silverstein, Ritz, & Jones, 1977; McClelland & Rumelhart, 1985; Sutton & Barto, 1981). The only technical rationale provided for a selectionist description of reinforcement networks is that the proposed neural mechanism "selects" the connections that most reliably coincide in time with reinforcement (Donahoe, Burgos, & Palmer, 1993, p. 28). As in other evolutionary analogies, a selective process is confused with a process of selection.

Taking their lead from Campbell's own "evolutionary epistemology" (1974), Donahoe and Palmer also state that their reinforcement models document processes of "variation," "selection," and "retention" parallel to those of evolutionary theory (1994, pp. 18–20). A closer look at how reinforcement networks actually function, however, shows that selectionist descriptions are misguided. First of all, these networks do not present the kind of variation that could feed into a selection process. The changes of activity in any given unit are transitory, purely temporal changes, which immediately rules them out as possible contributors to a selection process (cf. above). On the other hand, the network does present spatial variation, in the form of a set of different nodes and pathways. But this variation is never worked upon by any selection process, for the nodes and pathways neither die nor reproduce, even metaphorically. A reinforcement network of 10 nodes and 25 links before "selection," for example, will still comprise exactly 10 nodes and 25 links afterwards. Thus the proposed replicators do not replicate and cannot be submitted to sorting.

But the most serious confusion may involve the proposed mechanism of selection. In selection networks, behaviors are supposedly analogous to organisms (interactors) and neural elements to genes (replicators). Implementing this distinction was actually the rationale behind such networks (Donahoe, Burgos, & Palmer, 1993, p. 19). One would therefore expect the selection process of reinforcement networks to involve changes in the *interactors* and not the replicators. The distinction between interactors and replicators (Hull, 1980) was devised precisely to separate issues of interaction (phenotypic selection) from issues of replication (typically involving genes). *In reinforcement networks however, "selection" affects the replicator.* The "selection" step consists in changing weights of connections inside the network (Donahoe, Burgos, & Palmer, 1993), which is analogous to modifying the genetic material. This way of proceeding, in what nominally is a model of selection, infringes on the fundamental neo-Darwinian distinction between genetic variation (previous to sorting) and selection itself. Although the "selection" process of reinforcement networks is selective, in

the sense of affecting one neural connection rather than another, it cannot be analogous to natural selection at all. Instead it is suggestive of directed mutation.

Finally, in reinforcement networks the proposed interactors may not interact with the environment. Reading the operant selectionist literature (Donahoe & Palmer, 1994, p. 18, p. 32; Glenn & Madden, 1995) suggests that the interactors in operant "selection" are responses or environment-behavior relations. But, aside from the issue of drift already mentioned, the reinforced responses and environment-behavior relations virtually never *interact* with a reinforcing stimulus such as food. The latter is typically consumed *after* the emission of the operant response, and sometimes after an extended delay (e.g., Lattal & Gleeson, 1990). The possibility of delayed reinforcement seems to contradict the very notion of reinforced behavior as an interactor in a selection process; for two entities that do not even overlap in time cannot interact. Whereas any genuine interactor should overlap temporally with the selection agent, this condition virtually never holds in operant reinforcement. Hence here again, operant selectionism fails.

4. CONCLUSION

If our analysis is correct, the parallel evoked by Skinner (1981/1988) between operant reinforcement and natural selection is basically at odds with the facts. With or without its recent adjuncts, such as reinforcement networks, Skinner's selectionist analogy simply cannot account for many basic features of operant behavior, such as the existence of discrimination and delayed reinforcement. The analogy itself exemplifies recurrent confusions between the colloquial and technical uses of terms reminiscent of evolutionary theory. Purely temporal changes are said to document "variation," and a process that is merely selective is confused with a process of selection. In fact temporal variation can hardly feed into a selection process, and selection requires much more than selectivity. The most serious confusion involves presenting as selection what is actually reminiscent of directed mutation—granting the validity of such analogies for the sake of the argument. Finally, mere repetition is taken as analogous to reproduction, which it is not. Talking of reproduction or replication imposes some basic formal requirements on the dynamics of the processes at hand, basic requirements that reinforced behavior does not meet. All of the empirical evidence suggests that reinforced behavior repeats (e.g., McDowell, Bass, & Kessel, 1983) but does not reproduce, even metaphorically.

Note that the problems we raise involve no dispensable detail (such as the nonexistence of sexual reproduction in operant behavior), but rather

fundamental infringements on the neo-Darwinian principles of variation and selection that supposedly underlie the evolutionary analogy (e.g., Skinner, 1981/1988). A particularly puzzling aspect of operant selectionism is that the facts most clearly opposed to it, such as discrimination, are well known and have already been modelled without selectionist notions (e.g., Davison & Nevin, 1999). On the other hand, most of the variables that actually affect reinforced behavior have no clear equivalent in evolutionary theory, even at the vaguest metaphorical level (e.g., Davidson, Aparicio, & Rescorla, 1988; Dickinson & Balleine, 1994; Premack & Collier, 1962; Timberlake & Allison, 1974). What is the equivalent, in micro- or macroevolution, of three hours of water deprivation or of pairing a stimulus with reinforcement? Many of the resulting phenomena are beyond the reach of any selectionist metaphor. ("Selection" networks could probably model such phenomena, but we have already argued that these models present no coherent parallel with natural selection.)

The future of selection metaphors in behavior analysis remains unclear (Richelle, 1987; Smith, 1994; Staddon & Simmelhag, 1971). Operant reinforcement *mimics* some superficial features of natural selection by modulating response rate as a function of previous spatial and temporal relations. Because the mimicry does not extend to any shared causal structure, no detailed insight into behavioral causation is to be expected from selectionist analogies (cf. Amundson, 1989). On the other hand, limited uses of them are conceivable to the extent that they focus on the statistical properties of natural selection (Endler, 1986, pp. 4–5) and not its causal functioning. Vaughan and Herrnstein (1987), for example, have demonstrated formal parallels between frequency-dependent selection and the aggregated effect of some reinforcement schedules. These formal parallels merely concern issues of equilibrium, and are largely free of implications for the detailed study of operant processes (cf. Staddon, 1991). Progress in understanding the later will probably involve, and indeed already involves, nonexclusive analogies taken from a whole range of disciplines such as chemistry (Staddon, 1977a) and physics (e.g., Marr, 1992; Nevin & Grace, in press; Staddon, 1982).

Beyond any analogy, the difficult work of integrating behavior analysis and evolutionary biology remains to be done. Until recently the points of contact mainly involved foraging theory (e.g., Fantino & Abarca, 1985), but we can expect more varied attempts at integration in the future. These will necessarily explore a complex network of interactions among behavior, ecology, and evolution. Skinner's (1981/1988) preference for analogies over hierarchical integration has not proved very helpful in this respect. The difficulties we have identified in his approach may not generalize to others, equally metaphorical views (e.g., Campbell, 1974; Piattelli-Palmarini, 1989); indeed, it may not even generalize to Skinner's own selectionist view of

culture (but see Orr, 1996). Any claim to have established a similarity of process between natural selection and one psychological phenomenon or another should nevertheless be examined with critical care.

ACKNOWLEDGMENTS

We thank Nicholas Thompson for his helpful comments. We also thank the Secretaría de Educación Pública de México for generously supporting the 1998 Biannual Symposium on the Science of Behavior organized by the University of Guadalajara.

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Chapter 7

BEING CONCRETE ABOUT CULTURE AND CULTURAL EVOLUTION

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1. ABSTRACT

Culture consists of behavior. The units are practices shared by members of a group and acquired as a result of membership in the group. Although it is common to define the units of culture as abstractions, such as culturgens or memes, these abstractions in no way help to explain a group's practices. Instead, they only direct research away from the context and consequences that result in transmission of a practice from one group member to another. If culture is to be described as an evolutionary process, one must have a sufficiently general definition of "evolutionary process" to allow genetic evolution and cultural evolution to be examples. This may be accomplished by defining an evolutionary process as composed of variation (within a pool of replicators), transmission (by copying), and selection (by differential transmission). The replicators of cultural evolution are practices, which are units of operant behavior (i.e., behavior under control of consequences and context). Practices are transmitted from individual to individual by imitation and instruction. Instruction may be understood with the concept of a rule, which is a verbal discriminative stimulus (i.e., a verbally created context). Instruction consists of rule-giving, which results in rule-following on the part of the instructee. New rules come into a culture frequently as a result of rule-making, the generation of new rules on the basis of non-social

Perspectives in Ethology, Volume 13: Evolution, Culture, and Behavior
edited by Tonneau and Thompson, Kluwer Academic/Plenum Publishers, New York, 2000

stimuli. Selection in cultural evolution occurs because imitation and instruction of competing practices have differential consequences in the long run, consequences that impact reproductive potential. Since such long-term consequences have little effect on behavior, an adaptive practice (i.e., one that pays in the long run, called "self-control") is strengthened in the short-term by social reinforcers delivered by rule-givers. A behavioral analysis focuses on environmental events that are observable and, so, susceptible to research. The postulating of fictitious inner entities, whether they be memes, "devices," or "modules," only impedes understanding of culture and cultural evolution. Natural selection, because it is short-sighted and opportunistic, may be expected to produce mechanisms that aid and abet valuable behavioral functions. The key to understanding cultural evolution lies in understanding practices in the light of their environmental contexts and short- and long-term consequences.

2. INTRODUCTION

The main thesis of this essay is that culture consists of behavior and that cultural change constitutes an evolutionary process. I will argue that certain notions often advanced about culture are incorrect and misleading, because they divert attention away from cultural behavior. The units that make up a culture and pass from one individual to another within a cultural group or society are behavioral, and defining them as behavioral gives us a better picture of how cultural evolution works.

To understand cultural change as an evolutionary process, we need to understand cultural variation, transmission, and selection. I shall first take up cultural units, how they vary, and how to define them in a way consistent with behavioral definitions of culture. I shall then discuss the means of cultural transmission—imitation and instruction—pursuing a behavioral interpretation of instruction as transmission based on rules. Finally, I shall propose that operant reinforcement (Honig & Staddon, 1977) constitutes the means of selection in cultural evolution.

3. CULTURAL UNITS

Several authors have written about the units of culture. Dawkins (1989) called them "memes." Lumsden and Wilson (1981) and Pulliam (1983) preferred the name "culturgen." Boyd and Richerson (1985) used no new term, sticking to words like "phenotype," "variant," or "behavior,"

while also asserting, consistent with traditional social-science approaches, that culture consists of "information capable of affecting individuals' phenotypes" (p. 33).

Each of these definitions identifies the cultural unit with an abstraction possessing no specific properties. Boyd and Richerson's definition raises the question of just what "information" might be or where it might reside and how it might be "capable of affecting individuals' phenotypes." Pulliam (1983) writes, "A representation of each culturgen is stored in each individual's long-term memory . . ." (p. 428), apparently oblivious to questions about how and why such storage would occur or how and why something stored might be retrieved. Dawkins's (1989) meme, likewise, is a representation, "a unit of information residing in a brain" (Dawkins, 1982, p. 109) and transmitted from brain to brain.

3.1. Memes and Other Abstractions

These conceptions of cultural units raise at least four interrelated problems. The first one is superfluity. For example, Dawkins's (1989) meme is, for all practical purposes, redundant with the behavior it is supposed to cause. One observes that a behavioral pattern is imitated or instructed, and then that it repeats. The notion that the organism has acquired a meme from the imitation or instruction adds nothing to what has been observed, except the vague implication that the brain is involved. If Richard occasionally sings *Auld Lang Syne*, the meme is inferred from the observation that the song is sung, which is also the only evidence for the meme. It contrasts with the concept of the gene, which, although equally hypothetical at its inception, still summarized facts about heredity, such as: that the transfer occurs at conception, that some types dominate others, and that the recessive types nevertheless reappear in the next generation. The meme possesses no such explanatory power; instead it is the entity that must reside in the brain in principle, just because Richard sings *Auld Lang Syne*.

If the meme is merely redundant with the behavior pattern it is supposed to cause, and therefore is unnecessary, does that do any harm? It does harm because it distracts researchers from studying the behavior itself. Dawkins imagines memes competing in the brain, in the way of "early replicating molecules, floating chaotically free in the primeval soup" (1989, p. 196). As a result, he concludes prematurely that memes have no alleles. If instead we assume that what repeats is the singing of *Auld Lang Syne*, sometimes with errors, then other songs may compete with it in the behavior of an individual, as well as across individuals. Those competing songs are analogous to alleles, because they perform the same function (call it social bonding) as *Auld Lang Syne*. In general, two competing patterns of

behavior may themselves—not some hypothetical entities in the brain—be considered alleles if they are both ways of achieving the same end or function—if there is more than one way to "skin the cat." If the term "meme" referred to a function (getting a job done) in our culture, such as social bonding or looking attractive, then it would usefully associate different ways of bonding (singing together, drinking together, etc.) or different ways of looking attractive (wearing stiletto heels with a mini-skirt, wearing a sarong with sandals, etc.) as competing variants or alleles.

A second objection may be called "mysterious workings" (see Baum, 1994). Like any supposed representation, the meme as Dawkins conceives it is continuously present in the brain. Since the behavior it is supposed to cause occurs only occasionally, how does the meme cause the behavior? The situation is reminiscent of the notion that the rules of grammar somehow exist in the brain and cause utterances. The rules may determine some of the structure of the utterance, but they tell us nothing about the substance of the utterance or why it occurs at all. Similarly, the meme only represents the structure of a behavioral pattern; it tells us nothing about *when* and *why* the pattern occurs.

The notion of meme as an inner representation begs most of the questions that we need to answer if we are to explain the actual occurrence of cultural behavior. Why does this meme get stored and not some other? Why is it expressed in behavior only some of the time, and why on just the right occasion? These are really questions about the effects of past and present environment on behavior. The explanation of the behavior requires that we know its consequences, the context in which it is "appropriate" (i.e., the context in which it may be rewarded, for example), and the history by which that context came to control that behavior. Knowing the way behavior is "represented" in the brain might help, but it cannot substitute for an understanding of the way behavior is selected and facilitated by the environment.

A third problem is the falsity of the assumption that repetition requires representation. When behavior repeats from time to time, one may be tempted to assume that the behavior must be represented somewhere in the nervous system (e.g., Dawkins, 1989). Yet other natural events repeat—sunrise, sunset, the seasons, elections, and taxes. Every year during September and October, tropical storms arise in the Caribbean, yet no one suggests that these events are represented somewhere in the water or the air. When the conditions recur, the events recur. Why should it be any different with behavior? Every morning I brush my teeth; when the conditions recur, the behavior recurs. If Richard is at a gathering on New Year's Eve, his singing of *Auld Lang Syne* recurs. Ultimately, of course, the full explanation of both behavioral occurrences requires us to attend to the history of my tooth brushing and Richard's singing of *Auld Lang Syne*—how it was taught and how environmental cues came to control it. The relevance of

past events in no way necessitates memory as a stored representation (see Turvey, 1977; Watkins, 1990); behavioral patterns are probably more like storms than playback of recordings.

The influence of past events on present behavior doubtless explains much of the temptation to posit inner representations. People prefer to have their causes in the present, even if that means appealing to invisible causes. Memes as inner representations, however, create more problems than they solve, and raise pseudo-questions. If a representation is stored, then how is it retrieved? Who retrieves it, and why? The instruction, training, or experience that would explain the presence of the meme in the brain also constitutes an adequate explanation of the behavior, without the meme. The repeated circumstances that would explain the activation of the meme also constitute an adequate explanation of the repetition of the behavior, without the meme.

The compulsion to imagine inner representations also seems ironic. As genes are related to phenotype, so memes are supposed to be related to phenotype. Genes, however, unlike memes, cannot be said to represent phenotypic traits. Although DNA may be poetically referred to as the "blueprint of life," the most genes may be said to encode are the sequences of amino acids in various proteins (Dawkins, 1982). Beyond that, development is a complex sequence controlled by gene products and environment. Why should memes be different?

Which brings us to a fourth problem: the disanalogy between genes and memes. We understand that a gene in a parent is replicated in a zygote and then influences development of the offspring's phenotype. How would a meme be replicated? The environmental events—stimuli and consequences from other people—that would replicate the meme are the very same ones that would replicate the behavior. Understanding how the meme or the behavioral pattern is replicated requires an analysis of the same environmental influences. If Richard teaches a friend how to sing *Auld Lang Syne*, the song is now replicated in this friend, and Richard's cues and consequences explain the presence of the song in the friend's behavioral repertoire. More proximate stimuli and reinforcers will explain its occurrence thereafter on particular occasions (e.g., other people singing at a party and their approval in the form of friendly contact). Instead of a clear causal relationship like that between gene and phenotype, we have a sort of a muddle, in which the acquisition of the meme parallels the acquisition of the behavior and raises a chicken-and-egg problem.

These four problems also inhere in Pulliam's "culturgen" (1983) and in Boyd and Richerson's "information" (1985), with the exception that "culturgen" and "meme" could be redefined to refer to patterns of behavior, whereas "information" remains irremediably abstract. These criticisms, however, need to be offset by constructive proposals, focusing on concrete,

observable occurrences such as behavior and its environmental context. The proposal outlined here relies on principles of behavior analysis.

3.2. Proposal

To develop a coherent account of cultural evolution, we need first to define the concept of evolutionary process in a way that is general enough to apply to both genetic evolution and cultural evolution, in the spirit of Dawkins's proposal in the *Selfish gene* (1989). We may assume that any evolutionary process includes the elements of transmission, variation, and selection. The notion of replicator embodies the element of transmission—persistence through time as a result of copying. The notion of a pool of replicators embodies variation: within the pool, replicators that perform the same function but in different ways. Two alleles, for example, both of which affect coat color, may differ in the color of coat they promote. Selection occurs when some of the variations in replicators produce varied consequences in the environment that in turn result in varied copying success. It might seem a bit odd to put better predator avoidance or better resource acquisition in the environment, but they belong there because they are effects in the environment, along with a better nest, better parental care, and better manipulation of a host (see Dawkins, 1982). These environmental consequences feed back to affect the copying success of the replicators that promote them. Better consequences mean better copying success (cf. Baum, 1973). Differential consequences mean differential copying success, which is selection.

Genetic evolution is well understood as an evolutionary process. To understand cultural evolution as an evolutionary process, we need to answer the questions already answered for genetic evolution. What are its replicators? How are they transmitted? What is the pool of cultural replicators? How do the various replicators compete? And what is the principle of selection among variants?

In this essay I will argue that the analogue to genotype in cultural evolution is behavior itself. This will take some getting used to by evolutionary biologists, who are accustomed always to think of behavior as phenotype. If, however, we ask what actually gets replicated, what actually passes from one person to another, arguably it is behavior itself. The units of behavior that get replicated or passed along, I shall call *practices*. A practice like vegetarianism, for example, satisfies all of Dawkins's (1982) requirements for an "active germ-line replicator;" it is copied and promotes its own copying through its consequences in health and social affiliation. Calling the units practices helps to distinguish them from idiosyncratic patterns acquired by individuals and unavailable for replication (what Dawkins, 1982, calls

"dead-end replicators"). With Boyd and Richerson (1985), I include in culture all behavior patterns acquired as a result of membership in a group and exclude those acquired in other ways.

The pool of replicators, analogous to the gene pool, is the pool of practices that occur in the group and constitutes the group's culture. Another useful analogy might be to the genome, because practices, like genes, are interdependent. Selection may operate on clusters of genes or even the entire genome (Dawkins, 1982). The analog to the genome would be all the practices that occur in an individual's repertoire at a certain point in time (actually, a period long enough to be sampled, but short enough to be considered stable; see Baum, 1994).

Other analogies may be more difficult to draw. If practices are analogous to genes, then what is the cultural analog to phenotype? Perhaps it would be the culture's artifacts: art, technology, costumes, books, music, and so on. These are associated with a culture, but cannot be considered part of it. Rather, they are produced by practices of the culture, as a phenotype is produced by a genotype. A certain type of bowl may be distinctive of a certain culture, but the practice of making such bowls is part of the culture itself. Manufacturing practices produce artifacts like television sets, which in turn facilitate selection of other practices, such as entertainment, just as strong legs facilitate selection of patterns of capturing prey that entail running.

The parallels end there, however, because the relationship between phenotype and Dawkins's "vehicle" may be absent in culture. It seems inaccurate to say that the artifacts of a culture carry the practices as a vehicle carries replicators. Rather, it seems that the vehicle of cultural evolution would usually be the individual, just as in genetic evolution. (I say the individual rather than the group, because it would be an individual, for example, who would carry a practice from one group to another.)

In summary, in genetic evolution behavior is regarded as phenotypic, influenced by but distinct from the underlying genes—the replicators, the entities actually copied and transmitted. In cultural evolution, however, behavior itself is copied and transmitted; the replicators (the analogs to genes) are themselves behavioral units. When one person imitates another with good results, the behavior is replicated in the imitator, just as a parent's gene is replicated in a child.

3.3. Behavioral Units

B. F. Skinner (1981) suggested that the unit of culture is a contingency of reinforcement (a dependency of reinforcement on behavior in a certain context), one that is characteristic of the group and is social, in the sense

that one individual arranges consequences for the behavior of another. In contrast with the meme or culturgen, a contingency exists in the individual's environment. The context-behavior-consequence combination that constitutes a contingency is thus available for direct scientific study. As a unit, the social contingency has much in common with traditional views that define culture as a collection of transmitted values, because, Skinner (1971) argued, the behavior patterns that a group calls "good" consist of those that the group usually reinforces, and the patterns that a group calls "bad" consist of those that the group usually punishes (see Zuriff, 1987, and Garrett, 1987, for discussion of the ethical issues involved).

Skinner's concept of contingency contrasts also with meme and culturgen in that it points to the instructional practices of the group, rather than to the behavior instructed. It relates a religious practice, for example, to the reinforcement that strengthens and maintains it, to the punishment for alternative practices, and to the context, particularly accompanying verbal explanations, in which it is reinforced and not punished. In such a view, every cultural practice is tied to the instruction that produces it, because if the unit of culture consists in a social contingency, then defining any particular unit requires specifying a social context and socially mediated consequences. In Skinner's view, the analog to the genotype-phenotype distinction would be the distinction between the instructional practices of the group, which like genes might be said to "promote" the practices they shape, and the practices shaped by those instructional practices, which like phenotypic traits develop from the interaction between instruction and other environmental influences.

Which units should be included in a definition of culture depends on how broad the definition should be. Whereas some definitions, such as Skinner's (1981), aim primarily at elucidating human culture (Glenn, 1991; Harris, 1980), others potentially include cultural phenomena in non-human species (e.g., Boyd & Richerson, 1985). A definition broader than Skinner's would embrace not only instructional practices but also behavior acquired by imitation. For instance, an inclusive definition equates culture with learned behavior acquired as a result of group membership (Boyd & Richerson, 1985). That would include the example of sweet-potato washing spreading through a group of monkeys, which involves imitation but presumably no instruction.

4. TRANSMISSION

Although behavior may be transmitted also by imitation, Skinner's definition relies solely on instruction. Distinguishing between the two may

be crucial. The instructor both creates the context and supplies reinforcement for a cultural practice, whereas the model imitated provides only the context, and the non-social environment, or at least someone other than the modeler, supplies reinforcement. Washing sweet potatoes removes dirt and perhaps adds taste; the monkey being imitated has no influence on these consequences. Imitation induces the potato washing, but reinforcement of the behavior in no way depends on behavior of the individual imitated. In contrast, an instructor may model behavior, or induce it in other ways, and having induced it, reinforces it. A parent might show a child how to wash an apple and tell the child to wash an apple before eating it, but the social interaction cannot stop there, because the parent must praise the child for compliance, or at least withhold the punishment that he or she would administer for non-compliance. Of course, washing apples has non-social consequences also, such as long-term health, but these are usually too deferred to establish apple-washing (see below). Thus a more immediate reinforcer is required. The instructor supplies it.

The inclusive definition of culture (Boyd & Richerson, 1985) has the virtue that it allows for culture and its rudiments in animals, but has the weakness of glossing over the distinction between instruction and imitation. Some cultures may indeed be "imitation-only," whereas others also include instruction (Baum, 1994). Whether instructional practices occur in the cultures of species other than humans is an open empirical question. The inclusive definition, applied to human culture, reminds us that some behavior may be acquired by group membership without the need for socially mediated consequences, because the non-social environment supplies relatively immediate consequences. When one person eats what he sees another person eating, more often than not he has a good gustatory experience. If he eats the food and gets sick or discovers that it tastes horrible, he avoids eating it again. Even in this imitation-only acquisition, imitation cannot transmit behavior by itself, however; rather it induces behavior that persists only if it is reinforced. In instruction, too, the induced behavior persists only if it is reinforced, but instruction includes other means of inducing reinforceable behavior besides imitation, and the reinforcement is social.

In contrast with imitation-only acquisition, much behavior in humans is acquired as a result of contingencies in which both the context and the consequences are mediated socially. Imitation-only acquisition fails when the non-social consequences are too deferred to strengthen behavior in the short term. Learning to sing a traditional song along with a group of associates is reinforced immediately by signs of approval and acceptance (smiles, etc.), but the long-term advantages of affiliation, cashed out in the currency of reproductive success, are the key to understanding the existence of such reinforcement practices (that is, such short-term cultural contingencies).

4.1. Cultural Contingencies

To understand exactly what is meant by a contingency and to introduce the technical terms involved, let us consider an example. Herrnstein and Loveland (1964) trained pigeons in a discrimination that required them to peck at a response key if a picture contained a human being. The pigeon faced a panel on which the response key, operated by pecks, was mounted next to a small screen on which slides were projected from behind. Below, an opening to an electrically operated hopper allowed the pigeon access to grain for a few seconds. Slides were obtained from *National Geographic* magazine, and showed scenes from all over the world (jungles, deserts, cities, mountains), only some of which contained people (of all ethnic groups, dressed or undressed, old or young, in groups or alone). A slide was shown to the pigeon for a brief period, and if the slide contained a person according to the judgment of the experimenters, pecks at the key occasionally operated the hopper, allowing the pigeon to feed. If the slide contained no person, pecks were ineffective. After a few sessions with forty positive and forty negative instances shown in random order, the pigeons were pecking more often in the presence of the slides with people than the slides without. When the pigeons were well trained on the fixed set of slides, Herrnstein and Loveland began showing slides that the birds had never encountered before. The pigeons continued to discriminate between the slides with people and those without, even though every slide was new. Herrnstein and Loveland called the resulting discrimination a "concept," but we need only to consider a person in the slide as the context in which pecking was reinforced. Technically, a person in the slide would be called a *discriminative stimulus* (S^D); here I am using the word "context" as synonymous with "discriminative stimulus."

The example of "person" illustrates an important point about the context or S^D: It is a class of events, rather than a unique event. Although we have no idea exactly what cues distinguish person from non-person, the important point is that all the instances of person are functionally equivalent. They all signal the possibility of reinforcement, and they all have the same effect on behavior. It is well-known that such equivalence can be trained, even in pigeons (Vaughan, 1988; Wasserman, DeVolder, & Coppage, 1992). Had the example been a discrimination between a green light and a red light, the generic nature of the stimulus might have been less obvious, but even "a green light" varies from one occasion to another—it is viewed from various angles, ambient light may change, and line voltage may change. The stimulus always is a class of functionally equivalent events (Skinner, 1935/1961).

All three components (context, behavior, and reinforcement) of the three-term contingency have this generic character. One cannot sing a song

the same way twice; "singing *Auld Lang Syne*" names a class of events, not a unique event. Even a pigeon's key peck constitutes such a class, because the pigeon never pecks the key exactly the same way twice. Operant behavior patterns in general and cultural practices in particular are best viewed as classes defined by their environmental effects—by the "job" they "get done" (Guerin, 1997). Singing *Auld Lang Syne* may be a sub-category of the larger class "singing with a group," which in turn might be a sub-category of the class "affiliating with a group," which might often be the most useful level at which to characterize the behavior (Baum, 1995, 1997; Rachlin, 1994).

As the stimulus and behavior are generic and hierarchical, so too are the consequences. Even food delivery constitutes a class of events—the same food cannot occur twice. Smiles, nods, and vocalizations may all belong to the category "approval." It is probably of little importance whether some of these are fixed-action patterns and others more obviously modified by experience.

All three terms have also the property of temporal extension. The ways members of a group make pots, build houses, or adorn their bodies constitute practices characteristic of the group because they are prompted and reinforced by the group, even though no one could say these practices occur at any particular moment. Making a pot, building a house, or adorning one's body takes time. Similarly, the context and consequences of such practices cannot be said to occur at particular moments, but rather extend through time. The context for building a house in a certain way stretches over years and includes many events of instructing, modeling, and requesting, as well as presence of materials, tools, and tenants. The praise and appreciation one may receive for adorning one's body occurs intermittently and repeatedly, possibly over days, weeks, or years (Baum, 1997; Rachlin, 1994).

Similarly, in situations of instruction, in which the instructor supplies both the context and the reinforcement for appropriate behavior on the part of the instructee, the instructions, behavior, and consequences all are generic and temporally extended. The instructor may set the context by saying (and showing), "This is the way to shape the base of the pot," or "Do it like this," or simply "Look," and these are all equivalent in their effects on the behavior of the instructee. The instructor may reinforce by supplying a pat on the back, a vocalization like "Well done," or by withholding punishment. The context is set and re-set, in a variety of ways, again and again through time, and the consequences are supplied and omitted in a variety of ways, again and again through time.

Although the concept of three-term contingency allows us to understand acquisition of culturally appropriate (i.e., reinforced) behavior as a result of instruction, we still need to understand the behavior of the instructor. At a global level, instruction itself is a practice of the culture and

therefore may be instructed. In the short term, the appropriate behavior on the part of the instructee reinforces the behavior of the instructor. Viewed this way, instruction would coincide with verbal behavior in Skinner's (1957) sense, because the instructor would be seen as a speaker whose behavior is reinforced by the behavior of the listener (Skinner, 1957; Baum, 1994). The common practice of third parties' reinforcing instruction with money and goods reminds us also that the instructor's behavior is often valuable to the whole group. Why instruction occurs in the first place, however, and how it is valuable to the instructor and the group, cannot be explained just in terms of relatively short-term considerations. Evolutionary theory demands an ultimate explanation tied to fitness (i.e., gene replication).

4.2. Genes and Culture

For consistency with notions of selfish genes and extended phenotypes, we need to suppose that culture confers a benefit on genes that promote it. It performs a function that gives those genes an advantage over their alleles. But how could genes cause culture? And what function could culture perform that would feed back differentially to select genes for culture?

Genes may cause culture by promoting three phenotypic effects: sensory specializations, imitation, and social reinforcers. Sensory specialization is nothing new; it occurs throughout the animal kingdom to tune behavioral responses particularly to cues from conspecifics, prey, and other important features of the environment. Individuals typically respond only to mating calls and other courtship displays characteristic of their species, for example. No one should be surprised that humans' auditory systems are tuned particularly to speech sounds, that infants come into the world making phonetic distinctions, and that visual, auditory, and chemical cues from one person may cause physiological responses in another. Sensitivity to some cues generated by the behavior of other humans may be inherited from our pre-hominid past. Sensitivity to speech must have coincided with the development of verbal behavior.

The second phenotypic effect, imitation, may be viewed as an adaptation. Its occurrence extends beyond humans and primates, even to pigeons (Epstein, 1984). Boyd and Richerson (1985) argue that imitation confers an advantage as a shortcut to learning. In a species with relatively stable social groups, an infant or an immigrant who imitates will quickly learn to behave as the others do. If the behavior acquired by imitating group members is also adaptive within the particular environmental conditions, then genes that promote imitation will be selected over the alleles that fail to promote imitation. Correct foods will be eaten, predators and other dangers will be

avoided, and so on. Imitation plus stable social groups makes for at least the rudiments of culture in other species besides humans.

The third phenotypic effect, social reinforcement, is the key to instruction. Instruction would be difficult, if not impossible, without social reinforcers. They have the great advantages over tangible reinforcers like food of being constantly available, immediately presentable, and slow to satiate. They allow rapid interchange between instructor and instructee, resulting in rapid shaping of the instructee's behavior. We may suppose that the primary social reinforcers, such as smiles and exclamations, being fixed-action patterns, have a genetic basis. More importantly, the susceptibility to reinforcement by the cues produced would also have a genetic basis. How do the genes that promote these cues and the susceptibility to them cause culture? Once such cues can feed back on behavior differentially, to shape it, their employment becomes almost inevitable, because they offer their "users" virtually endless opportunities to manipulate the behavior of others for selfish ends. More technically, altering the behavior of others often provides reinforcement for the behavior that achieves the altering. As a result, such "manipulation" should be strengthened and maintained in members of the group.

The susceptibility to reinforcement by social cues ("docility") should nonetheless be seen as adaptive (Simon, 1990). It is presumably selected because it benefits the genes of its possessor. Having your behavior manipulated by other group members is good (within limits). That is one way to understand the virtues of imitation; when A imitates B, A's behavior is manipulated by B's, but A benefits. Similarly, when B instructs A in some useful way, A benefits, even though B benefits too and might be said to manipulate A's behavior. The mother who teaches her child good hygiene manipulates the child's behavior, but the child's genes stand to benefit as much as hers do.

In sum, the answer to the first question—how genes cause culture—is that by providing three basic elements (sensory specialization, imitation, and social reinforcement), they ensure its development. The behavior of a child or an immigrant placed in a group in which those three elements exist will be shaped into the group's practices. Useful new practices that arise will spread, and will do so automatically. Psychology textbooks abound with examples of research in which a group of total strangers organizes itself and brings the behavior of its members into line in a matter of hours, if not minutes. The sensitivity of human behavior to cues from other humans is such that manipulation and organization are inevitable.

The second question—what biological function culture performs—is more complicated. A general answer is implicit in the notions of "shortcuts to learning" and "useful practices." A more specific answer must focus on what is learned and why it might be useful. To be beneficial, behavioral

patterns must make contact with important long-term consequences that affect the copying of genes. But how is such long-term beneficial behavior acquired, when the consequences are so deferred?

The short answer is, "Rules" (Skinner, 1969; Baum, 1995). A discriminative stimulus produced by the behavior of an individual who may also supply consequences (up to now called the "instructor"), and whose behavior is reinforced by appropriate behavior on the part of a second individual (up to now called the "instructee"), is a *rule*. This term allows us to get away from talking about "manipulation" and "instruction," with a gain in precision. It reminds us that a culture is as much characterized by what group members say to one another as by non-verbal products like pots, televisions, and airplanes.

For example, in the United States the slogans that appear on license plates are often revealing. Maine's plates say on them "Vacationland," reflecting the economy's dependence on tourism, and Massachusetts's say, "The Spirit of America," probably advertising its prominent role in American history. New Hampshire's citizens, contrary to the surrounding states, choose to put personal advice on their plates: "Live Free or Die." This slogan gives a hint of the local culture, and sheds light on some of the state's peculiarities, such as the absence of any personal income tax or sales tax, and, with a population of less than a million, its possession of the third largest legislative body in the world.

Slogans, like other rules, are stimuli, produced by the behavior of a speaker and controlling behavior of a listener. They accomplish nothing by themselves, but the behavior they control, which I shall call "rule-following," achieves important ends—ends that impact reproductive success. The importance of those ends also lends a similar, if less direct, efficacy to the types of behavior that produce rule-following, which I shall call "rule-giving" and "rule-making" (Baum, 1995). Rule-following, rule-giving, and rule-making are the key to understanding what the units of culture (practices) are, how they are transmitted, what function they perform, and how they are selected.

4.3. Rule-Following

In all cultures, children are taught to obey adults (Simon, 1990). Rule-following is reinforced massively and repeatedly. The child who fails to learn to follow rules fails in all walks of life, and the parents who fail to teach rule-following are considered negligent. These commonplace observations point toward consequences of rule-following beyond the short term. If a child learns to wash fruit before eating it because the parents give the rule and reinforce the behavior, it is equally true that the parents provide

instructions and reinforcement for the sake of the child's long-term health and reproductive potential. This explanation of rule-following and rule-giving hinges on the ultimate consequence of enhanced gene copying.

Rule-giving arises because the long-term consequences of reproduction-enhancing behavior, such as washing fruit, are too deferred to reinforce the target behavior (Rachlin, 1995). In the short run, washing fruit takes time and effort, costs that militate against its occurrence. The socially mediated consequences act to overcome these immediate costs. The situation is more challenging still when misbehavior—detrimental to reproductive potential in the long run—is immediately reinforcing, and socially mediated contingencies need to overcome the "temptation" to obtain the short-term reinforcement. However nutritious fresh fruits and vegetables are in the long run, junk food tastes better.

Figure 1 details the problem created by the effects of delay on reinforcement. Even though a consequence like good health might have tremendous effect or weight (V_L) when presented immediately (at time *c*), the more delayed this consequence is, and in general the less obvious it is, the less its effectiveness (Logue, 1988). At time *b* for example, when the consequence is off in the future (i.e., delayed), it is much less effective, and at time *a*, still less so. The curve relating value to delay is called a *discounting function*, and is well known to approximate a hyperbola (Logue, 1995). Because of value discounting, a relatively minor consequence like sweet taste (V_S) that follows behavior shortly (time *b*) is much more effective than a major but delayed consequence. At point *a*, when both consequences are discounted, the large, long-term reward is preferred, but as point *b* draws near, when the small, short-term reward will be available, preference switches (e.g., Ainslie & Herrnstein, 1981). This local switch causes a

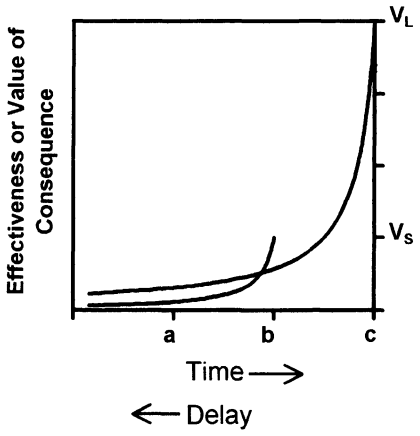

Figure 1. The effects of delay on the value of consequences. A large reinforcer's immediate value (V_L) at time *c* is discounted at earlier times *a* and *b*, when it is delayed. Consequently, a small reinforcer's value (V_S) may exceed the value of the large reinforcer at time *b*, when the small reinforcer is immediate and the large reinforcer is delayed. This creates a problem in self-control. If a choice could be made at time *a*, when both reinforcers are discounted, no problem would arise, but such commitment is usually impossible. The discounting functions are known to approximate hyperbolas.

dilemma; one may take the small, short-term reward, even though one's best interest is to wait for the large, long-term reward. One may choose to spend money on a small item now instead of saving toward a large goal, or one may choose to avoid the dentist now instead of avoiding major dental work in the future.

Pigeons, for example, faced with a choice between immediate 2-s access to food versus 4-s access delayed by 4 s, almost invariably choose the immediate 2-s reinforcer (Rachlin & Green, 1972). When they are allowed to make their choice at an earlier time, however (point *a*), they choose the larger reinforcer. Humans, faced with similar choices, behave similarly (Logue, 1995). The behavior of choosing the large, long-term reward is termed *self-control*, whereas the behavior of choosing the small, short-term reward is termed *impulsiveness*. *One of the principal functions of culture is to promote self-control in the face of choices that affect reproductive potential in the long run.*

Figure 2 diagrams the short-term and long-term contingencies in one situation calling for self-control. On the one hand, in the presence of junk food (S^D_I) we have the impulsive tendency to eat junk food, with the minor,

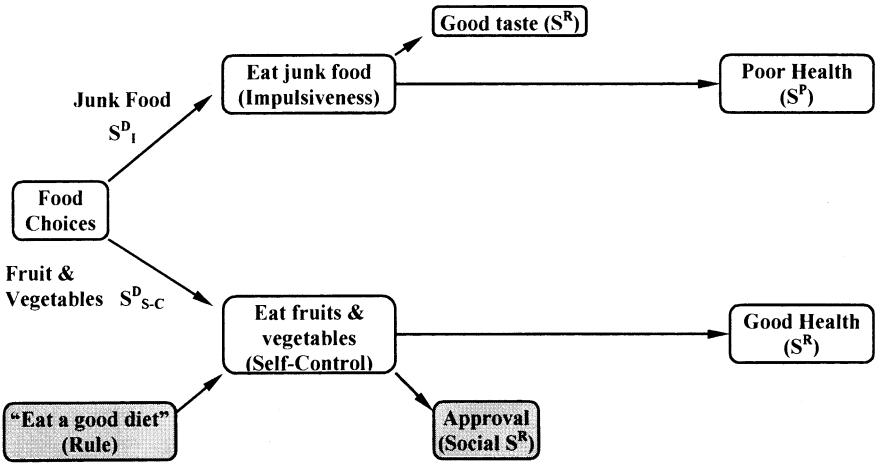

Figure 2. A typical problem in self-control offset by the rule an instructor gives; a cultural contingency. The choice is between impulsiveness, which produces minor reinforcement immediately (short arrow) but major punishment in the long run (long arrow), and self-control, which produces major reinforcement in the long run. The instructor gives the rule, a verbal discriminative stimulus, which induces the behavior of self-control, and also gives immediate social reinforcement, which counteracts the minor immediate reinforcement gained by impulsiveness. The result is that self-control occurs even without any opportunity for prior commitment.

short-term reinforcement of good taste (S^R, short arrow) and the long-term, major reproduction-reducing outcome of poor health (S^P, long arrow). On the other hand, in the presence of fruits and vegetables ($S^D_{S\text{-}C}$) we have a perhaps weaker tendency to eat healthy food (self-control), with the long-term major reproduction-enhancing outcome (S^R) of good health (Rachlin, 1995).

Research on self-control demonstrates that for humans faced with the sort of choice shown in Figure 2, the frequency of eating junk food would be high and poor health would be likely, if no other intervention occurred. As the shaded boxes in Figure 2 illustrate, however, another contingency may be operative. Just as immediate good taste may function as a powerful reinforcer, so immediate social reinforcers like approval may have great power. A rule such as "Eat a good diet" enhances the tendency to eat fruits and vegetables (self-control) because in its presence the relevant behavior is followed by approval (social reinforcement S^R). The relatively minor but immediate social consequence may overcome the relatively minor but immediate taste consequence, leading to the major long-term consequence of good health. Fostering self-control in the face of the temptation to impulsiveness is one of the main functions of rules, their more general function being to foster adaptive behavior.

To understand rule selection, we must assume that rules compete. Suppose some group members some of the time give the rule "Eat what you want, but just avoid carbohydrates." This rule would compete with "Eat vegetables, and avoid excess fat and sugar," implicit in Figure 2. Following either rule may result in weight loss, a potentially health-enhancing outcome. Following the latter rule, however, might ensure ingestion of essential vitamins and minerals. If, over time and people, the "Eat vegetables" rule results in better health, following that rule will increase in frequency, and following the competing rule will decrease in frequency.

The tendencies to give the competing rules will change similarly. Giving the "Eat vegetables" rule will increase in frequency, while the frequency of giving the other rule will decrease, because the reinforcement of rule-giving derives from the instructee's rule-following and thus indirectly from its long-term consequences. The situation depicted in Figure 2 really contains two social contingencies: an explicit one, governing rule-following, and an implicit one, governing rule-giving. Since rule-giving is as much operant behavior as rule-following, rule-giving must be reinforced; reinforcement is provided by the instructee's rule-following (Skinner, 1957, 1969).

By the same token, Figure 2 illustrates two different kinds of cultural practices. A first kind is the "garden-variety" practice (rule-following), the sort that might be spoken of as just "what we do." The second kind is an *instructional* practice, rule-giving, that results in transmission of the garden-variety practice—imitation being the other means.

4.4. Rule-Giving

The contingencies governing rule-giving are harder to discern than those governing rule-following. We may begin with the relatively simple case of rule-giving among relatives. Why does a parent tell a child to wash his hands before eating? It seems clear that the parent is concerned with the child's welfare, and indeed we may observe further that parents too little concerned with their children's welfare would be selected against. Thus, the ultimate reason for rule-giving is the enhancement of the reproductive potential of both the rule-giver and the rule-follower. The proximate reason is that rule-giving (giving instructions, orders, requests, advice) is reinforced by the compliance of the rule-follower (cf. Alcock, 1998).

Recognizing the consequences of rule-giving tells only half the story; we need to discover also the relevant context or discriminative stimulus (S^D). Most people in the United States have little direct experience with relationships between illness and washing fruit before eating or between illness and washing hands. They rarely say, "Wash your hands so you will stay healthy." Instead, they talk about "dirt" and what is "nice" or "right." The environment is too clean for the connection to be obvious. It only becomes so when Americans travel to places like India, where one may see open sewers, fruit in the market covered with flies, and people in the street who clearly are ill. Since these sights are hidden from most Americans, their rule-giving has to be based more on what they hear from others than on their own non-social experience. We teach our children to wash their hands before eating because we were taught by our parents to wash our hands before eating. Technically, the context (S^D) for most rule-giving consists in other rules, verbal stimuli produced by other people—such as "Good parenting includes teaching a child good personal hygiene" (Guerin, 1992).

4.5. Rule-Making

Rule-giving is part of culture (the particular rules given distinguishing one culture from another), and rule-giving is transmitted from person to person within a cultural group, but someone has to be the first to give the rule. The first-time utterance of the rule has to derive from the non-social environment. A more detailed analysis requires us to consider how a behavior-consequence relationship that is obscure, because it must be seen either over time or across people, may come to control formulation of a rule new at least to the speaker. This form of new-rule-giving may be called *rule-making*.

The basis of rule-making is recognition of repetition. Before we learn to make rules, we learn to categorize events. We come to name occurrences

such as "upset stomach," "fever," "winning," "losing," and so on. The reinforcement for such naming resembles the reinforcement for other rule-governed behavior; it is socially mediated by the behavior of people who say, "This is a shoe," "Do you see the shoe?," "Please bring me the shoe," and later, "Is your stomach upset?" and "Did you win the game?" (Horne & Lowe, 1996). Later still, we begin to name conjunctions of events, such as "I ate too much, and I got an upset stomach" or "Billy worked really hard and got an A." These episodes form the basis for what are commonly called "causal inferences" and that I am calling rule-making.

Let us consider a simple example, the discovery of dental hygiene. It may be a particularly revealing example, because the relatively recent incorporation of tooth-brushing in American culture at the group level may parallel one's experience as an individual. My parents, coming from Old World families, never acquired the habit of tooth-brushing and also never demanded that I brush regularly, but they made sure that I visited the dentist once a year. Inevitably, I had cavities that required filling, some years only a few, some years many. Over the course of several years, I began to notice a pattern to this variation: The more carefully I brushed, the fewer the cavities. Figure 3 summarizes the experience in a chart. It includes another discovery: If I stopped eating candy and drinking soda, the annual

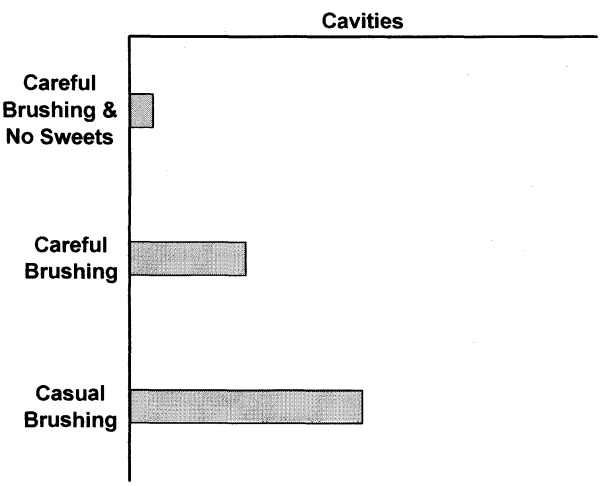

Figure 3. An example of a behavior-consequence relation that may act as a discriminative stimulus controlling rule-making. Variation in behavior (tooth-brushing and eating sweets here) covaries with variation in consequences (cavities here). The whole aggregate of conjunctions functions as a discriminative stimulus as a result of a history, usually specifically trained, of examining such data and formulating conclusions (i.e., making rules).

number of cavities fell to an even lower level. The first comparison resulted in an increase in the frequency and care with which I brushed. The second comparison resulted in a large decrease in my consumption of sweets.

Such changes in behavior as a result of behavior-environment covariation may be viewed as the shaping of behavior by environmental consequences. The way that tooth-brushing was reinforced by a reduction in cavities, and consumption of sweets was punished by continued cavities, mirrors what one might expect even in a non-verbal organism, although probably over a less extended time span. Only when the covariation affected my verbal behavior could we state unambiguously that I made causal inferences from my experiences. Only when I began to preach about the virtues of tooth-brushing and the evils of sweets, which I referred to as "tooth rot," might we incline to say that I engaged in rule-making.

Still, however, we should hold back on calling it rule-making, because another step is required: transmission—at least of the behavior, but also, following Skinner's reasoning, transmission of a social contingency; that is, transmission of the triad, rule plus behavior plus rule-giver-mediated consequences. My friends soon tired of hearing my sermons about brushing and sweets, and punished the behavior by calling me "Old Rot Tooth." My children, however, were in no position to respond this way. I taught them all to brush their teeth at the earliest possible age and exhorted them to be sure to brush regularly and well. As adults they all brush regularly, and they have had almost no cavities. (The absence of cavities may also be due to fluoridation of the water in the town where we lived, but this only shows that a rule may cease to be supported by someone else's experience in the future.)

The real proof of rule-making, however, occurs when it becomes rule-giving in the next generation. My oldest daughter is now teaching her four-year-old son to brush and is exhorting him as I did her. Since she lacks direct experience with cavities and her only experience with tooth-brushing is the result of my rule-making and consequence-supplying, we may conclude that her behavior now constitutes rule-giving.

How do we explain rule-making and its transmission as rule-giving with the concepts at hand? First, rule-making is trained; it is operant behavior. It builds on the naming of conjunctions already discussed, as when children are asked questions like, "Did you have fun in the park?" and "What did you like best there?" These in turn lead up to questions asking "why" ("Why do you like the zoo?") and answers using the word "because" ("Because I like the monkeys.") Although rule-making requires no formal education, such training constitutes one important function of schools. Children are trained to make causal inferences and to draw conclusions from data: "Why do you think the plant we kept in the sun is doing fine, whereas the plant we put in the dark is doing badly?" Correct inferences may be reinforced with praise and high grades. As a result, most citizens are adept

at rule-making by the end of high school. Those who attend college get further training, and those who go into the sciences get still more.

Like all operant behavior, rule-making is under stimulus control. Skinner (1953, 1957) regarded the behavior of scientists as primarily the formation of discriminations. The relevant discriminative stimuli are called "data." They consist not of a single event, but of a succession of conjunctions like those represented in Figure 3. The entire series of visits to the dentist, in which the variations in tooth-brushing and sweets-consumption correlated with variations in number of cavities, increases the likelihood that eventually I will say, based on patterns shaped in school, that brushing teeth regularly and well leads to fewer cavities.

Figure 4 illustrates the relationship between rule-making and rule-giving. The top line depicts rule-making in general. The second line illustrates how the entire set of events in Figure 3 stands in the place of a

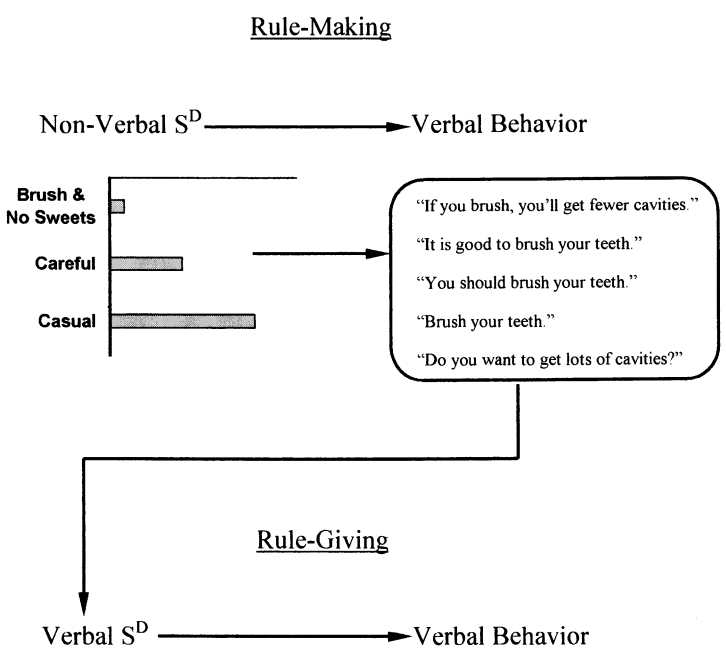

Figure 4. How rule-making leads to rule-giving. Top line: In rule-making, a non-verbal discriminative stimulus (S^D), in the form of a behavior-consequence relation, induces verbal behavior, in the form of a class of functionally equivalent utterances. Second line: an example of a behavior-consequence relation and the class of utterances it induces. Third line: The utterances produce (vertical arrow) verbal discriminative stimuli functionally equivalent to one another in that they induce the same verbal behavior (an instance of giving a rule, such as in Figure 2).

discriminative stimulus (S^D). The latter controls a class of verbal behavior including declarative forms ("If you brush, then you'll get fewer cavities") and other functionally equivalent variants (some declarative value judgments, some exhortations, some commands, and even some questions). The third line shows how this class of verbal behavior produces a class of verbal discriminative stimuli, heard by the next generation, which control the same verbal behavior as in the original rule-making, but now released from its non-verbal origins (Guerin, 1992).

Although the discussion of rule-making and rule-giving so far might seem to suggest that the rules tend to be "true," rules need not be veridical. First, a rule may just be wrong. Based on incomplete data, one may draw an incorrect conclusion that is corrected later. The medical profession may first recommend blood-letting as a treatment and later repudiate it. Second, the function of a rule may differ from its surface reading. A rule like, "If you eat pork, God will punish you," needs to be examined in the light of the actual consequences of pork avoidance in this world. It probably represents a type of rule related to group cohesion and segregation, functionally equivalent to, "If you are to belong to this group and reap the benefits of membership, then you must behave so" (Guerin, 1998). Rules of that sort enable members to identify one another and to avoid squandering resources on people who are unlikely to reciprocate (Dawkins, 1989).

4.6. Rule-Giving and Altruism

We can now address the question of why rule-giving occurs between non-relatives. Rule-giving is a form of altruism (Dawkins, 1989; Simon, 1990; Wilson, 1975). It costs the speaker little and benefits the listener (rule-follower) greatly in the long run. If the two actors are unrelated, the rule-giver's reproductive potential may be enhanced eventually by reciprocal rule-giving from the listener or other members of the group. I may tell you where to get a good buy on automobile tires today; you may advise me about the best schools for my children tomorrow. In more everyday terms, group members share useful information with one another, to their mutual benefit in the long run.

The delays in reciprocal altruism open the door to cheating, usually failure to reciprocate. In rule-giving, however, another type of cheating is possible: The speaker may give the listener advice that will harm the listener in the long run. The speaker does so "knowingly" when reducing the listener's fitness in the long run reinforces the speaker's false rule-giving. Such behavior accords with the competitive aspects of evolution, because one way to increase the relative fitness of one's genes is to reduce the fitness of the genes of one's competitors. Accepting the minor cost of giving

misinformation in return for a large reduction in the competitor's well-being would be called spite (Wilson, 1975). Individuals guard against spite by discriminating between immediate group members and strangers, between those whose rule-giving is likely to be helpful and those whose rule-giving is uncertain. As one interacts repeatedly with another person, this person's rule-giving eventually comes to exert strong stimulus control over one's rule-following or none at all. This fact of life is summarized in the saying, "Fool me once, shame on you; fool me twice, shame on me" (a rule about rule-following).

4.7. Units, Transmission, and Selection

In sum, the replicators in cultural evolution are the behavioral units that I have called "practices." A cultural practice is a unit of operant behavior, whose full definition includes not only a class of actions, but also the relevant context and reinforcement. As Figure 2 illustrates, the context of a practice is often a rule, and the reinforcement is socially mediated (e.g., approval). If the behavior occurs enough, the long-term contingency may take over. In such cases the relevant context for behavior becomes the non-social discriminative stimulus labeled $S^{D}_{S\text{-}C}$ in Figure 2 (fruits and vegetables). Although some psychologists would say that the rule has been "internalized," all that has occurred is a transfer of control from an obvious, proximate contingency to an extended or ultimate contingency. The person who is spontaneously kind to strangers has not "internalized altruism;" rather, his behavior has come under control of social contingencies in which altruism is ultimately praised and materially rewarded with status and its accompanying opportunities. Control remains in the environment (for further discussion and experimental evidence, see Logue, 1995).

Transmission of cultural practices occurs in two ways: imitation and instruction. Imitation is probably the less important of the two for human culture, because it relies on non-social consequences to strengthen behavior. Its scope is limited in comparison with instruction, which, because it relies on contrived contingencies and social reinforcers, opens the door to endless innovation. Instruction depends on a history of obedience training and transmits a practice by inducing it with a rule and reinforcing it when it occurs. Besides this rule-governed behavior itself, the practice of instructing the behavior (rule-giving) is also transmitted. Social reinforcement is often arranged for rule-giving. Not only are people encouraged to use birth control, some of them are also instructed in how to encourage others to use birth control.

Finally, practices are subject to selection because some function better than others. Practices may be selected in clusters, just as other replicators

are, because they are interdependent and perform several related functions. Extended families, for example, might foster arranged marriages: too many individual's lives are affected by a marriage to leave the relevant decision to the bride and groom. Whether selected individually or as a cluster, however, practices are selected by their consequences. Whichever practices are more reinforced than their competitors (alternative ways of performing the same function) increase in frequency. They increase in the behavior of individuals, as when an artist gradually shifts toward non-representational painting or a scientists finds more and more occasions to speak of selfish genes, and they increase across individuals, as when new students come out of art schools painting non-representationally, or when new students come out of graduate programs already speaking of selfish genes.

5. SELECTION

To understand the selection that goes on in cultural evolution, it is essential to identify the reinforcers that do the selecting. If these reinforcers were arbitrary, culture could evolve in any direction, independent of the human genome and perhaps even antithetical to it. Dawkins (1989) proposed such a view. Boyd and Richerson (1985), in contrast, argued that cultural evolution cannot but be ultimately limited by natural selection. It may wander widely, but it wanders within confines set by the phylogenetic history of our species, because the reinforcers that control human behavior are far from arbitrary.

5.1. The Importance of Reinforcement

Both fixed-action patterns and operant behavior depend on contingencies in the environment. The difference is that the contingencies to which fixed-action patterns are adapted were stable enough to make contact with genetic selection, with the result that fixed-action patterns are relatively immune to the vagaries of short-term environmental variance and are available at crucial times, such as in the presence of a predator or a potential mate. Fixed-action patterns depend only on context, in the form of releasers, and have no need of consequences. Operant behavior, in contrast, is shaped by consequences within a lifetime, and therefore is highly sensitive to short-term changes in contingencies. Operant behavior may nevertheless originate in fixed-action patterns. For example, a baby gull's pecking at its parent's beak may improve because it produces food more

reliably, thereby turning into operant pecking (for a general discussion, see Teitelbaum, 1977).

The ultimate consequences of the cultural practices pointed to in Figure 2—health, resources, relationships, reproduction—which affect the replication of genes, are usually too deferred or extended to influence operant behavior within a person's lifetime. Feeling healthy, acquiring a mate, amassing resources, and establishing friendships are all results of continued effort over extended time periods. They often exist as alternatives to shortsighted, impulsive behavior and therefore call for self-control (Rachlin, 1995).

The advantages of self-control provide a role for social reinforcers, which presumably result from our ancestors' history of living in groups. Boyd and Richerson (1985) suggest that culture originated initially in the advantage conferred by being able to learn from others in a variable environment. A child growing up in a group or an adult joining a group might do well to behave as those around behave. If such a tendency allowed rapid adaptation, it might also open up additional reproductive opportunities, and genes that favored it would spread. Those genes would promote manipulation of their vehicles' behavior by other group members (Dawkins, 1982).

So a possible first stage in the evolution of culture would be imitation reinforced by non-social reinforcers, as in non-human primates. Exactly how the transition from this first stage to manipulation by social reinforcers would have occurred is unclear, but it probably happened as a result of the advantages of opening behavior to manipulation, coupled with advantages to the manipulator (Simon, 1990). How good for a parent to be able to shape a child's behavior with reinforcement and punishment, to adapt it to whatever the environment requires! How difficult to do that without reinforcers and punishers that are convenient, low-cost, and immediate! If the result benefited one's children, thereby benefiting the parent's genes, the genes for susceptibility to parental cues as consequences could spread. Once established, anyone in the group might be able to benefit by manipulating the behavior of others with those same facial expressions, intonations, and so on. Those reinforcers and punishers would become the dominant means by which cultural practices were established and transmitted. Indeed, no one could live in a group and fail to have his behavior shaped toward group norms. Besides making culture possible, social reinforcers and punishers make culture inevitable.

Once we appreciate the importance of reinforcement and couple it with the idea of stimulus control (context), it becomes neither necessary nor likely that the recurrence of cultural practices depends on internal representations such as memes. Whatever the underlying neural basis for the recurrence of operant behavioral patterns might be, it is unlikely to resemble the mechanism for a fixed-action pattern. Sensitivity to consequences

guarantees that cultural practices, like all operant behavior, involve more or less constant feedback in the form of interaction with the environment (Baum, 1973, 1989).

Unfortunately, some scholars writing about culture, failing to recognize the role of behavior-environment feedback, treat behavior as if the environment released it in an input-output fashion. They thus postulate not only representations, but also miniature machines, called "devices" and "modules," that somehow produce behavior as a result of environmental inputs. The results have been disastrously misleading.

5.2. Devices and Modules

Let us consider a well-worn example: the so-called language acquisition device, which has become standard fare among cognitive psychologists (e.g., Pinker & Bloom, 1992). Each child is supposed to possess this device and to acquire language because of it. The device is supposed to take input from the environment (heard utterances of speakers) and to process it into the rules of grammar and a lexicon of meanings. With their help, a person becomes able to decode utterances heard and to encode utterances to be generated.

Pinker (1994) and others have made good use of the idea of a language acquisition device to argue that language is an adaptation, a product of natural selection (Pinker & Bloom, 1992). This is an important point, because it allows a richer understanding of the origins and functions of language. The point could have been made without the language acquisition device, but insofar as the notion helped, it was useful. That, however, is as far as its usefulness goes.

The criticisms of the meme made earlier apply to the language acquisition device in full force. Even if it really did extract grammar and meaning from the heard utterances, it would leave unanswered the questions that most need answering: why language is useful and why particular utterances occur. The language acquisition device tells us nothing of the behavior of speaking and its consequences.

The notion of the language acquisition device is not only unhelpful, however; it is positively misleading. Its pernicious effect lies in supposing that it is a unitary mechanism that might itself perform a function. Tooby and Cosmides (1992), in their lengthy critique of the standard social science model, emphasize that natural selection cannot produce organs serving general purposes. As a product of natural selection, the brain ought to consist of a collection of many special-purpose adaptations, for selection is opportunistic and must make do with whatever variation at hand. It can select only what is there and immediately useful. In other words, natural

selection has no foresight and cannot plan ahead for contingencies other than the ones actually occurring in the environment. Hence its adaptations tend to be cobbled together, rather than elegantly designed.

This argument applies not only to the brain, but also to the language acquisition device. Rather than producing a unitary mechanism, natural selection would produce a collection of more specific adaptations—modifications to sensory systems, to effectors, and possibly portions of the brain—all of which aided the acquisition of language. The result would be less a unitary mechanism than a motley crew. Pinker and Bloom (1992) and Tooby and Cosmides (1992) nod toward this point, but treat it as trivial. They imply that the only issue is whether the device is localized or distributed. They miss the larger implication that a motley crew cannot perform a function; rather each member arises to aid and abet some function that is being performed. The usefulness of that function provides the basis for selecting its aides and abettors.

What function is being aided and abetted? Actually two partially independent functions (often lumped into "language acquisition") are aided and abetted: the acquisition of spoken language and the acquisition of receptive language, which correspond to verbal behavior and stimulus control by verbal stimuli. Language or verbal behavior is undoubtedly useful; it allows a speaker to manipulate the behavior of a listener for the good of both their genes. It is essential, however, to remember the difference between verbal behavior and other communication schemes. Courtship in birds and pheromones in insects offer instances in which creatures communicate and may be said to manipulate one another, but the consequences of the manipulation operate only in the course of natural selection across generations; they cannot alter the fixed-action patterns involved during the lifetimes of the individuals.

Verbal behavior, in contrast, is operant behavior; it is controlled by its consequences. It depends on reinforcement and punishment (Moerk, 1996). A person who speaks Spanish and English speaks each language only with those who understand it. Why? A person in need of the salt requests it of the person across the table. Why? The answers to such questions cannot be found in the language acquisition device or the motley crew of aides and abettors; they are to be found in the history of consequences in context that led up to the utterances. If the language acquisition device could perform the function of language acquisition the way it is said to, it would be possible in theory to put a child in front of a television set for two years and at the end have it speak the language heard. One need not do the experiment to know it would fail. When I was a child, my parents often spoke Yiddish in my presence. They did so because I couldn't understand; Yiddish was their secret language. Even though I heard it often and was motivated to learn it, I never acquired Yiddish. Hearing it had an effect; I was able to

make the non-English sounds better than my classmates when I studied German and Russian in college. But I never learned Yiddish, because my parents only spoke it to each other, never *to me*. Verbal behavior depends on and consists of interaction with the environment. The adaptations produced by natural selection only make it certain that verbal behavior and verbal stimulus control will be acquired. They take care of the selective attention, raw material, variation, and social consequences required.

Similar criticisms apply to the "modules" that Tooby and Cosmides (1992) assume to be produced by natural selection. They list a variety of modules that are supposed to perform all sorts of functions, from mate selection to detection of cheating. Perhaps the most extreme example of a misleading imaginary module is what they call the "theory of mind" module. As with the language acquisition device, this module is supposed to take input from the environment and convert it into a theory, not of grammar, but of others' minds. Translated into behavior, this notion means that people behave (mostly talk) as if other people possessed minds—meaning inner thoughts, intentions, and beliefs. It comes down to observations such as the following: (a) Tom's seeing Jane pause and then initiate action, followed by his saying that Jane was "thinking;" (b) Tom's seeing Jane persist in behavior that customarily has produced particular results, followed by his saying that Jane is "trying to achieve" these results; (c) Tom's hearing Jane talk about God and seeing her go to confession, followed by his saying that she is religious. Other people's behavior provides cues that guide our behavior, notably our verbal behavior. Such social cues could be important enough that special sensitivity to them was selected, because effective social behavior could avoid rejection and open up opportunities for reproduction. But to attribute the sensitivity and the talk about mind to a "theory of mind" module seems gratuitous. Worse, it substitutes for the study of various behavioral facts a line of fruitless speculation about what the "theory of mind" is like (Baum, 1998; Heyes, 1998).

There is no substitute for an understanding of the interaction of behavior with the environment over time. Imaginary inner devices and modules cannot take the place of understanding the effects of reinforcement and punishment in shaping people's behavior in general, and shaping cultural practices in particular.

6. CONCLUSION

The notion that the units of culture and cultural transmission are stored somewhere in the brain is both inaccurate and misleading. The units passed from one group member to another consist of behavior—more

accurately, operant behavior in context. Like any operant unit, a cultural practice thus contains three terms: a context or discriminative stimulus (S^D; a model or a rule), the effective behavior (defined as the class of variants that accomplish the particular consequences), and its consequences (the class of outcomes produced by the behavior in that context). Since copying transmits cultural behavior itself, an analog to genotype in cultural evolution must consist of behavioral units. The analog to phenotype might consist in the products of cultural practices. Contrary to Dawkins's account, this behavioral view contains an analog to alleles in the various competing ways of achieving a common result.

Practices may be distinguished on the basis of their mechanism of transmission (whether by imitation or by instruction; i.e., rule-following) and on the basis of their type of reinforcement (socially mediated or not). Imitation-based transmission occurs when a model provided by one group member induces similar behavior in another, and the imitator's behavior is reinforced automatically by environmental consequences, without intervention from the modeler. Instruction-based, or rule-based, transmission occurs when an "instructor" gives a rule (a verbal S^D) and also supplies immediate reinforcement of the behavior appropriate to this rule. Although practices transmitted by compliance or rule-following depend at least for a while on socially mediated reinforcement, they may eventually come under the control of long-term, environmentally based reinforcers more directly related to reproductive success. Both aspects of the instructor's behavior, rule-giving and consequence-supplying, constitute verbal behavior in Skinner's (1957) sense, because they are reinforced by the instructee's (the listener's) appropriate behavior or rule-following. The behaviors of rule-giving and rule-following may depend on socially mediated reinforcement in the short term, but must ultimately enhance reproductive success. Particular rules dominate in a culture if in the long run they enhance reproductive potential more than their competitors do.

Although novel practices may enter a culture by immigration or by mutation due to copying errors, a more reliable source is the behavior of rule-making, in which sequences of events or relations in the non-social environment play the role of discriminative stimuli for the verbal behavior of the rule-maker. If a subset of the group engages in rule-making, new practices will enter the culture on a regular basis, and then persist if they produce reinforcers ultimately tied to reproductive success. Their spread among non-relatives, however, must depend on rule-giving that is a form of reciprocal altruism. The benefits of "sharing information" (i.e., reciprocal rule-giving) tend to accrue to all group members, whether genetically related or not.

Understanding all cultural phenomena thus depends on an understanding of the role of reinforcement and punishment. Cultural practices are

tied to natural selection because the reinforcers and punishers that shape them were selected in the course of our species' phylogeny. Low-cost social reinforcers and punishers not only made culture possible; they made it inevitable. Many other adaptations have been selected to aid and abet the process of shaping by consequences; these in no way take the place of that interactive process. Casting them as "devices" or "modules" only detracts from an understanding of the development and transmission of cultural practices.

ACKNOWLEDGMENTS

The author thanks F. Tonneau, N. Thompson, and R. Hinde for many helpful comments.

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Chapter 8

INTENTIONALITY IS THE MARK OF THE VITAL

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ABSTRACT

Much of the philosophy of mind has been dedicated to reconciling the mental with the material. But to the extent that the "mental" is seen as equivalent to the "intentional" and the "material" as equivalent to the "biological," the project of reconciling the intentional with the material is unnecessary. Concepts exhibiting the special logical properties thought to be unique to intentionality are a commonplace in biology. Thus, the special problem of the emergence of intentionality in human evolution, in human conscious and language, and in human culture is neither special nor of problem: in the relevant logical respects, intentionality is, and—has always been immanent in the simplest of biological systems.

1. INTRODUCTION

Franz Brentano is often cited as the origin of the view that "intentionality is the mark of the mental," that is, that "all mental phenomena

Perspectives in Ethology, Volume 13: Evolution, Culture, and Behavior
edited by Tonneau and Thompson, Kluwer Academic/Plenum Publishers, New York, 2000

exhibit intentionality and no physical phenomena exhibit intentionality." (Dennett, 1981, p. xvii–xviii: Chisholm, 1967). For Brentano, and for the many philosophers and scientists influenced by his seminal *Psychologie vom empirischen Standpunkt*, mental events had a distinct form of existence and the distinguishing feature of that form was intentionality.

Much of what has been written in the philosophy of mind since Brentano has been dedicated to reconciling the mental with the material. For many, this project has been construed as reconciling the intentional with the biological, explaining how intentionality emerges in the course of the evolution toward the human species, in the operations of the human brain, in the development of the human individual, and in the meanings of human cultural elements. The goal of this essay is to demonstrate that, to the extent that the "mental" is seen as equivalent to the "intentional" and the "material" as equivalent to the "biological," the project of reconciling the intentional with the material is unnecessary because concepts exhibiting the special logical properties thought to be unique to intentionality are a commonplace in biology. Thus, the special problem of the emergence of intentionality in human evolution, in human conscious and language, or in human culture is neither special nor a problem: in the relevant logical respects, intentionality is, and has always been, immanent in the simplest of biological systems.

2. THE PROBLEM OF INTENTIONALITY

When Brentano used the word "intentional" he was using the term in a very special sense. In ordinary language, an "intention" is an idea of the future that moves us to action. In cognitive psychology, "intentional" is synonymous with "goal directed." Both of these understandings of "intentional" are valid within their own context, but neither is precise enough to make clear why Brentano's dictum had such an impact on psychology as an explanatory science. Brentano used the term "gerichtetsein" to mean "directed toward an object" or, one might say, "laden with about-ness" (Brentano, 1874; Dennett, 1987, particularly, pp. 271–2; Rosenberg, 1988; Dennett & Haugland, 1987). In the framework of Brentano's Psychologie, an intentional state must be "directed-toward," or "about" some object external to the state itself. An explanation is intentional in this logical sense if it accounts for events by reference to mental (and so, and thus, intentional) state as a cause. An intentional cause is identified by a verb of mentation (explicit or implicit) that takes as its object and is specified by some proposition. Schematically, such an explanation claims:

A did D because A desired (wanted, believed . . .) that [x].

where [x] may be any proposition about the world.

Most intentional explanations attribute an event to some combination of intentional states, typically to an agent's desires for a state of affairs and its beliefs that some set of deeds will achieve that state of affairs. For example, The professor drank a glass of water because he wanted to clear his throat and he believed that drinking a glass of water would clear his throat.

Here, the desired state of affairs is a clear throat and the deed, drinking, is said to be caused by the combination of this desire with the belief that drinking water will effect it.

To the extent that psychologists and other social scientists invoke human beliefs, thoughts, and wants to explain human behavior, their explanations are intentional in this logical sense. This fact may be bad news for social scientists because explanations that are intentional in this sense have logical properties that are thought to alienate them from the natural sciences in general and from biology in particular.

For example, if you saw me drinking a liquid that you knew to be chablis, you would be entitled to infer both that some chablis exists in the world and that the beverage in my glass has the properties of chablis. From those inferences, you could develop a host of testable hypotheses whose corroboration could be easily connected to established physical laws. You could, for instance, conclude that the contents of my glass had a particular density, boiled at a particular temperature, and froze at a particular temperature. Suppose, however, that you do not know that I am drinking chablis, but only that I believe I am drinking chablis. Now the warrent for your previous inferences collapses. And in compensation for this lost set of testable empirical hypothesis, you are left only with questions: was the substance in the glass really chablis? Was it even a liquid? Was I even drinking? And even if you confirm that the glass actually did contain chablis, you will not be entitled to infer even that I believed it to contain white wine, since—from the facts stated—you have no way of knowing whether I know that Chablis is a white wine.

In general, intentional explanations, even if they embody true propositions about beliefs, thoughts, wants or feelings regarding [x] entail nothing about [x]! This implicative opacity of intentional explanations comes in two forms—referential and existential. Both kinds of "opacity" involve an inability to "see through" a proposition to the "meanings or facts" that presumably "lie behind" it. (Rosenberg, 1988, 1967). "Existential opacity" (more commonly called "intentional inexistence" by philosophers) refers to our inability to infer the existence of a believed-in happening or object from the fact that somebody believes in it. People do, after all, believe myths. "Referential opacity" refers to our inability to infer even the content of the believed proposition from the fact that the proposition is believed, since the content of the proposition is dependent on what the believer "means by it." People do, after all, understand the words they use in very different ways.)

Most social scientists and philosophers have responded to the problems raised by intentionality in one of two ways. The first way, favored by Brentano, has been to accept the dualistic thesis that intentional propositions describe events in a very special, immaterial place called the mind. For some, this view has the advantage of immunizing human free will from material determination. But, for social scientists, it has the disadvantage that it irrevocably separates human psychology, and, perhaps, all human and animal behavior, from the causal laws and theories of the natural sciences. If intentional "causes" are immaterial, they can play no part in the casual system studied by the natural sciences. Nor can they be investigated by the natural scientific techniques which presume that system as their basis.

The other option, favored by some contemporary philosophers of mind, is to claim that mental states just "are" brain states. This "brain-state identity thesis" seems to reconnect mental states to the causal networks of the natural sciences, but it creates a new problem. Those philosophers who argue that intentional states just are brain states recognize that no particular combination of neural events is necessary for any particular intentional state. Thus, while a particular sequence of neural states may be said to constitute a particular intentional state, many other combinations of neural events may constitute the same intentional state. In fact, the number of neural states that are sufficient for a particular intentional state may be virtually infinite. Far from being daunted by this many-to one relation between neural and intentional states, some identity theorists have embraced it as the supervenience of the mental upon the neural.

In recent years, enthusiasm for the concept of supervenience has been formidable and authoritative (See, Sober, 1984; Depew & Weber, 1997, who use the concept to defend the concept of fitness from accusations of vagueness and circularity.) But for practicing behavioral scientists to embrace supervenience would be a serious error. For most scientists, statements asserting that "A causes B" are among the most heuristically fertile hypotheses available for investigation. Such a statement implies that A is antecedent to B and is necessary, sufficient, or both necessary AND sufficient for the occurrence of B. Because they have these meanings, statements asserting casual connections are heuristically pregnant with suggestions for experiments to determine contingencies between A and B.

Using the notion of supervenience to connect intentional events to natural causes, however, drains the claim that "A causes B" of its heuristic power: first, because A can never be more than one of an indeterminately huge number of neural states, no one of which is ever necessary for B; second, because tools adequate to determinately specify the structure of A are not and may never be available to practicing scientists; third, because—having putatively reduced intentional states to neural states—we are

methodologically discouraged from exploiting the interesting fact that people seem remarkably adept at recognizing each others' intentional states despite their complete inability to detect neural states. And finally, even if supervenience could specify exactly which neural states were responsible for intentional action, it would not have solved the problem of the origin of intentionality, since it does not tell us how neural states ever become intentional in the first place.

Fortunately, a third option is available, that avoids both the causal disconnection of dualism and the heuristic disconnection of supervenience, and that leaves us free to exploit our capacity to recognize intentional states in others. This third option is to treat intentional states, for the purposes of scientific investigation, as neither events in the organism's mind nor states of its brain, but, rather, as properties of the relation between the organism and its environment: i.e., as higher order properties of the behavior of the organism. On this approach, most "intentional explanations" are (as Hempel and Oppenheim concluded in 1948) not causal explanations at all; rather, they are, scientifically interesting and heuristically fertile descriptions of the objective design of an organism's behavior (Thompson & Derr, 1995). This third possibility is developed in this paper.

3. INTENTION AND DESIGN

Both in their behavior and in their structure, organisms exhibit a property that corresponds to what we mean when we speak of the "design" of a building or of an automobile or of a computer system. This property is commonly and properly referred to as "natural design." The word "design" is sometimes used metonymously to refer to the process of designing, but we use it to refer exclusively to properties of a designed product.

Natural design properties are of a higher order than more conventional properties such as mass, color or shape. But applying the term "design" (adapted from engineering) to the behavior and morphology of animals does no more invoke vitalism or pan-mentalism than Darwin's use of the term "selection" (adapted from English animal breeders) invokes anthropomorphic creationism. Design properties are found in the complex relations among organisms and their surroundings; they are both objective and empirical. They posit no new realm of being, and they claim no exemption from the laws of the natural sciences.

Identifying design properties involves scientists in a process that is a mirror image of reduction. A concept is said to have been reduced when a theorist demonstrates that it can be entirely explained by lower-level (and often less glamorous) phenomena. We commonly think of reductions as

moving from higher to lower levels of organization, as when we say that adaptation is just a change in gene frequencies or when we say that motivation states are just states of the hypothalamus or that heat is just kinetic energy.

Since the description and study of natural design involves the scientist in precisely the opposite sort of conceptual movement, namely, a movement from a lower to a higher level of organization, the natural design approach recommended here might be thought of as "up-reductionism". From the natural design point of view, many biological and psychological terms that are construed as genetic or neural explainers of behavior can be reconceptualized as behavioral describers. For example, adaptation is reconceptualized as a property of the relationship between the form of organisms and their circumstances, rather than as just another name for natural selection. Motivation is treated as a property of the relationship between variations in behavior and the circumstances in which that behavior is deployed, rather than as just another name for a neural state specifiable only by its effects. Finally, development is conceived as a stable property of the relationship between a growing organism and its environment, not as the unfolding of some genetic program.

3.1. What Is Natural Design?

In the world of engineering, design is a systematic association between an array of structures and an array of circumstances in which those structures are deployed. In a design, the association between those arrays is such that no matter what the circumstance, if the structure associated to that circumstance is deployed, the result is constant.

For instance, consider the design of the wrenches in a mechanic's tool set. The set contains a series of specialized wrenches, each appropriate to one of the circumstances the mechanic encounters, each fitted to the form of a particular type of bolt or nut. Provided that the correct wrench is deployed, the result is constant: the bolt or nut turns. Watching the mechanic turn a bolt with a wrench, one might say that THIS wrench is well designed for turning this particular bolt. But the correct attribution of design implies more than the fitness of THIS wrench to turn THIS bolt. It means that there is a systematic relationship between the form of the many tools in the set and the many circumstances in which they are employed, such that when the "right" wrench is used on the "right bolt", the bolt usually gets turned. THIS wrench is exemplary of that relationship and so it is said, briefly, to be well designed. Thus, design is a holistic property: it can be attributed to one item in the array (the individual wrench) only because we recognize that item as an element in one of two coordinated arrays. And design properties, as properties of the relation between those arrays, are higher-order

properties than the mass, shape, or malleability of the individual wrenches or bolts in those arrays.

When the same holistic property is manifested by organisms or their behavior, it is called natural design. Natural design is an association between an array of organ forms, behaviors, or artifacts and the array of circumstances in which they are deployed. But because of the temporal and physical scale of these arrays, natural design becomes evident only when one applies a patient program of comparative analysis to natural phenomena.

For instance, to observe phylogenetic design, one might emulate Darwin and take a five-year cruise around the world on a small overcrowded warship with Lyell's principles of Geology as one's only light reading, get off the boat at every opportunity to escape seasickness and the moody fundamentalist with whom one is cabined, collect specimens of basically different creatures in similar environments and of basically similar creatures in different environments, taking careful note of their origins, and then pour over one's collections for 20 years looking for correlations between the form of organisms and their life circumstances.

To observe motivational design, one might like Tinbergen spend several years in the field observing members of a species, carefully prepare a catalogue (an ethogram) of behaviors performed, of the circumstances under which they are performed, and the consequences of their performance both for the actor and others, pore over your field notes grouping behaviors that occur under similar circumstances and produce related consequences, and then perform a series of experiments using the method of dual quantification to confirm your inferences.

To observe developmental design, one might like Piaget painstakingly observe the change in the behavior of children and the coordinated changes in the expectations of the world around them. From these observations, one might note patterns of correspondence between the child's behavior and the world's expectations. Associating these patterns with the typical ages at which they occurred, one might call them "stages."

These historical examples emphasize that natural design is not the sort of property detected by a single crucial experiment or highly focussed field investigation. In fact, the research programs that make important natural designs evident are so sustained and disciplined that they seem as much to be the result of character as of than method. Nevertheless, the result of such research is the discovery of natural design properties which, although located at a higher level of organization, are every bit as objective and empirical as mass, length, or valence.

3.2. How Is Natural Design to Be Explained?

The existence of natural design requires explanation. Most (but not all) natural designs can be explained as the product of control systems

(Bowlby, 1969/1982; Powers, 1973a, b). Over time, control systems generate an array of actions, each of which is associated with an element of an array of circumstances. The pairings of circumstance with actions all have the common feature of producing a common outcome: maintaining specific features of the circumstances near reference values.

Of course, not every natural process that tends to stabilize an empirical variable is a control system. Many natural feedback processes regulate variables but are not control systems. For example, the presence of slush on the ground tends to regulate the temperature of the air near the surface at around 32 degrees. At temperatures above 32 the ice in the slush melts, absorbing calories and cooling the air. At temperatures below 32 the water in the slush freezes, releasing heat and warming the air. Such feedback processes are not control systems because, although they do regulate a variable within certain fixed limits, they are not designed to regulate it: the relationship between the elements in the involved arrays can be exhaustively described and explained without the discovery or deployment of any higher-level design properties. Natural selection is such a natural feedback process.

Control systems are distinguished from simple feedback processes because they are designed to achieve their effects. A control system may be said to be designed when it is one of a set of integrated control systems each of which is deployed in a characteristic circumstance and all of which, working as a supersystem, achieve a common outcome for the organism or entity of which they are part. The organs of the human body display natural design in this sense: each of them regulates some physiological variable and all of them, collectively, maintain the life of the whole organism.

Organic control systems may exhibit natural design in another sense as well: the reference value guiding one control system can itself be the output variable of another control system. This kind of design is seen in the water regulation system of the human body: the system varies the tone of the blood in response to a reference value which itself varies with the long term availability of water (Jones et al., 1991).

In short, from the perspective of natural design, organic nature consists of a hierarchy of control systems, each a designer of systems or activities at a lower level and each designed by activities at a higher level. At the top of this hierarchy (on pain of avoiding an infinite regress), must be a process which is capable of producing natural design but which is not itself designed. That process is natural selection. In each generation, natural selection assesses a complex property of an organism, its "adaptedness", and adjusts that property in the next generation of the population of which that organism is a part. Because natural selection is itself a simple feedback system, it is a non-designed designer.

The term "non-designed designer" has a long history in cultural controversies over the relation between evolutionary science and religion,

controversies that are irrelevant to our present purposes. The claim that natural selection does not itself exhibit natural design is a scientific hypothesis. If true, it neither confirms nor refutes the theological hypothesis that natural selection exhibits (or is the result of) non-natural design. Both "Creation science," and "scientific atheism" seem to miss this elementary logical distinction.

4. CONTROL SYSTEMS AND INTENTIONALITY

The goal of this essay, you will recall, is to demonstrate that the problem of the emergence of intentionality in human behavior is no problem at all because intentionality ("about- ness" in Brentano's formulation) is imminent in the simplest of biological systems. We have so far argued that organisms have natural design properties and that these design properties are the consequence of the operation of control systems. If we can show that at least many of the natural design properties produced by control systems exhibit the logical features of intentionality, our argument will be complete.

To understand how control systems can engender intentionality, we have to examine control systems in greater detail. For ethologists, John Bowlby's account of control systems is most useful (1969/1982). Bowlby was concerned to construct a theory of parent/child interaction that replaced a behaviorist theory with one that was based in biology in general and ethology and control systems theory in particular. Bowlby's theory was particularly influenced by the manner in which infants respond to variations in their social environments. For example, once an infant has formed a relationship with a primary caregiver, that infant will suffer behavioral deterioration during a long term separation from the caregiver and then exhibit intense clingyness when the primary caregiver returned.

In Bowlby's control system analysis, infant and mother form a system in which the infant uses various behaviors (e.g., crying) to control the proximity of the mother. The control of proximity, in turn, makes it possible for the infant to control its access to food, warmth, and protection from harm. In Bowlby's analysis of attachment, there are two control systems at work: one is the system that controls maternal proximity; the other is the meta-system that monitors and evaluates the effectiveness of the proximity-control system. During long term separation, both systems fail; hence, when child and mother are reunited, the infant must reestablish, and test both the proximity-control system and the meta-system. The re-calibration of this meta-system is what the parent experiences as "clingyness."

The model for Bowlby's work was a biological control system. In Bowlby's terminology, all control systems, have the effect of moving some

variable toward a set point. Bowlby uses the term "set-goal" for set point, defining it as

> Either a time-limited event or an ongoing condition either of which is brought about by the action of behavioural systems that are structured to take account of discrepancies between instruction and performance. In this definition, it should be noted, a set-goal is not an object in the environment but is either a specified motor performance, of short or long duration, between the animal and some object in or component of the environment. Thus the set-goal of the peregrine's stoop is not the prey stooped at but interception of that prey. In the same way, the set-goal of some other behavioral system might be the continuous maintenance by an animal of a certain distance between itself and an alarming object in the environment. (Bowlby, 1969/1982, p. 69)

In Bowlby's theory, the operation of a biological control system is always related to a particular environment in which that system evolved and to which it is adapted. He writes:

> In the case of biological [control] systems, structure takes a form that is determined by the kind of environment in which the system has in fact been operating during its evolution, an environment that is of course usually, though not necessarily, much the same as that in which it may be expected to operate in future. In each case, therefore, there is a particular sort of environment to which the system, whether manmade or biological, is adapted. This environment I propose to term the system's "environment of adaptedness." Only within its environment of adaptedness can it be expected that a system will work efficiently. . . . It is important to recognize that an environment of adaptedness exists not only for each species but for each single system of each species; . . . (*op cit*, p. 47)

In its environment of evolutionary adaptedness, the operation of a biological control system will produce a predictable outcome. Because of specific features of that environment of evolutionary adaptedness, achieving the set-goal normally brings about just those particular consequences for which the behavior has been selected. Thus, Bowlby's theory makes a sharp distinction between the set-goal of a behavior (the set of effects that the control system tends to bring about, such as the maintenance of a constant distance from a threatening object) and the function of a behavior (those effects for which the behavior has been selected, such as the avoidance of predation).

The distinction between the set goal and the function of behavior systems has remained as a foundational principle in the field of ethology, and has been called "The Law of Short- Sighted Striving" or "Lorenz's Law" (Thompson, 1986a). Konrad Lorenz (1935/1957) played an important role in further explicating the curious disjunction between the goals of an animal's behavior and the functions of that behavior. He attacked MacDougal's (1921) concept of instinct precisely because it seemed to imply

that animals were aware of the good they did for themselves by pursuing their goals. Many of the phenomena so memorably described by Lorenz and the other classical ethologists—the English robin that would display to a bit of red fluff on a wire, the goslings that would follow Lorenz in his hip-waders, the goose that would retrieve a giant egg, the stickleback that would display to a postal van—are clear evidence that animals will strive to achieve a particular set goal even when that set goal has been decoupled from the functional situation.

But Lorenz's Law is an example of a more general principle regarding control systems. To respond to a perturbation in the variable it regulates, the system must assess that variable in some way. And characteristically, the system does not directly assess the variable that it regulates, but instead assesses another variable, the cue variable, that is coupled to it (Powers, 1973a,b). For instance, a household heating system uses the bending of a bimetallic strip as a cue to assess (indirectly) the temperature of the house. A home heating system is a control system that regulates air temperature to a preset temperature by controlling the operation of a furnace. The bending of the bimetallic strip works as a cue because, within the range of temperatures that corresponds to our environment of evolutionary adaptedness, the bending of the strip is closely correlated with temperature of the air around the strip. The system's reliance on this cue can be demonstrated by mechanically bending the bimetallic strip: by applying slight pressure to the strip, one can induce the furnace to turn off before the ambient air temperature has reached the setting on the thermostat. Similarly, the body's respiration system uses blood acidity as a cue to blood oxygen content (Fulton, 1958). The system regulates the level of oxygen in the blood to a stable value by controlling the breathing rate of the organism. The cue, blood acidity, works because the metabolic conversion of oxygen to carbon dioxide acidifies the blood. The reliance of the blood-oxygen control system on this cue can be demonstrated by manipulating blood acidity directly. For example, the administration of very large doses of antacid tablets often reduces the air hunger of persons with high altitude pulmonary edema.

Cues play a similar role in the behavioral control systems that so fascinated classical ethologists. For instance, for male english robins, the configuration, "red-tuft-on-wire" is a cue that regulates territorial defense behaviors. The cue works because, in the natural evolutionary environment of a male robin, the only stimulus corresponding to the pattern "red tuft on stick" is another male robin. The reliance of the male robin territorial behavior on this cue can be demonstrated by inducing territorial behavior with a "red-tuft-on-wire" cue that is decoupled from it's normal accompaniment, a male robin. For instance, by providing a tuft of died cotton mounted on a twist of straight brown wire, one can induce defense

behaviors in a territorial male robin. Similarly, one can inhibit a male robin's defense of territory against another male robin by dyeing the feathers of the intruder green. (Tinbergen, 1951; Lack, 1953) The clear theme that runs through all these examples is that the cue variable of a control system "stands in" for the functional variable that the control system regulates. Thus, to know that C is a cue to F, we must not only show that C and F are correlated in the relevant evolutionary environment, we must also demonstrate that in the operation of specified control systems, C "stands in" for F. This means that the cue relation is not a simple relationship between objects in the world (C and F), but a second order relationship between (i) the relation of C and F in an environment, E, and (ii) the relation of an organism or system to that same environment. Thus, the minimal statement required to specify a cue relation is: Variable, C, is a cue to functional variable, F, for the System, S, in Environment E.

The fact that the cue relation requires reference to a control system for its specification has the important consequence that certain kinds of statements about cue variables will exhibit the implicative opacity of intentional propositions. If you know that a male robin inhabits your garden, you can reliably infer that you have a living bird in your garden and that the bird can be expected to behave in certain ways. But if you know only that cues to the presence of a male robin have been found in your garden, you cannot reliably infer that any object in your garden is a male robin or will behave like a male robin or even that male robins have not gone extinct. As classical ethologists often demonstrated, the cues to biological events are not infallible predictors of the events itself.

The implicative opacity of the cue relation becomes particularly dramatic when we consider a situation in which the same object provides a cue for two different control systems. Imagine a situation in which a cat is stalking a male robin that is, at the same time, intruding into the territory of a second robin and displaying at that robin. And imagine further that we can observe the cat and the second robin, but not the first. For the territorial male second robin, the intruding first robin provides a cue—red tuft on brown wire—of the existence of an intruder. In some sense, we would like to say that the cat responds to the same first male robin; but for the cat, both the cue variable and functional variable are different. For the cat, the first robin provides a cue—twitchy small object—of the existence of a prey object. Thus, while both the cat and the second robin are responding to cues provided by the first robin, which inferences we are privileged to make depends on which of the two "observers" we consider. If we see the cat, then we are entitled to believe that the cat is responding to a small twitchy thing. We are not entitled to any inferences about red breasts. If we see the second robin, we are entitled to infer that it is responding to the

configuration "red fluff on wire." We are not entitled to any inferences about twitchyness. And in neither case can we infer, with certainty, the existence of the first robin.

Thus, to determine the implications of a cue attribution, we have to see the world from the point of view of the specific control system of which the cue relation is part. This would not surprise Jakob von Uexkull (1934/1957), who claimed that every biological process, no matter how elementary, approaches the world from a "point of view," that is, selects from the array of all possible physical stimuli only those few that are relevant to its interests, and then acts to alter the world in ways favorable to those interests. A "point of view" in von Uexkull's sense is an objective property defined by the variables to which the control system of an organism responds and the variables which the system attempts to manipulate in the interests of that organism. A "point of view" is both intentional AND objective.

5. SO WHAT IF INTENTIONALITY IS AN OBJECTIVE CHARACTERISTIC OF ALL BIOLOGICAL SYSTEMS?

In the course of their evolution, a social predator (such as a lion, a wolf or a human being), will survive and reproduce largely to the extent it can anticipate the behavior of other organisms, such as conspecifics, prey, and rival predators. The work we have done so far in this essay gives us a simpler way to identify the skills of a wise predator. Such a predator would be greatly aided by knowing the intentions of the other organisms with which it must deal. But this doesn't mean that it must somehow intuit some image of the future that lives in some non-material mind space of the other. It means only that it needs to know, for at least one of the control systems of the other, what cue variable that system reads and what behavior it is designed to regulate.

Imagine the problem of a lion trying to figure out how to catch a gnu. One afternoon the lion is returning to its den after finishing off the remains of a small impala. It encounters a gnu on the path near the water hole, but, not being hungry, it does not give chase; it merely notes the fact that drowsiness following its consumption of the impala has preceded the presence of gnus at water holes.

Suppose now that the next time the lion passes by the remains of an impala (or the next time it is drowsy), it starts looking for a gnu. Such a lion will soon starve because it would be using impala remains or lion drowsiness as incorrect cues to predict the gnu's presence. What the lion needs to know is what cue variable the gnu uses to regulate its approach to the water

hole. And this variable presumably has nothing to do with lion drowsiness or impala remains.

How is the lion to discover this variable? By observing gnus. The lion should retire to the top of a kopje overlooking the water hole and note the comings and goings of gnus. He should engage in a kind of comparative analysis, analogous on a small scale with what an ethologist does when he tries to discover what the goal of a behavior is. He should note the conditions that obtain each time the gnu comes to the water hole and which of those conditions also occurs when the gnu doesn't come to the water hole. By this method the lion can isolate which factors within the EXtension of "gnu-comes-to-the-water-hole circumstances" constitutes its INtension from the point-of-view of the gnu.

The advantages of such observation may explain why predators, such as lions, sometimes observe their prey when they are not hunting. The well designed lion will get the gnu when he, the lion, has discovered the intention of the gnu's coming to the water hole . . . say, to cool off in the heat of the day. Presumably, he has done so by evolving some sort of a cognitive module designed for intention-detection—a device that compares and contrasts the concomitants of prey movements until it isolates the cues for those movements which are used by the control systems of the prey animals themselves. Thus, the fact that intentionality is a property of control systems—and therefore of animal behavior—should lead us to expect that animals who associate with other animals will develop elaborate cognitive devices for detecting this property in their associates.

Like lions, human beings are highly evolved design detectors. As a consequence of our evolutionary history as hunters, as prey, as members of social groups, and as warriors against other social groups, we have evolved to be especially good at detecting natural design properties in the behavior of other systems. Detecting designs in others helps us adapt our own behavior to those designs or take action to change the designs of those systems. (Inflicting rewards and punishments are two techniques by which we often redesign the systems with which we interact.)

Of course, dealing with designed and non-designed systems requires entirely different strategies. If you are dealing with a non-designed system, a change in your behavior is likely to get you a change in result. But if you are dealing with a designed system, particularly a system that is designed to deal with you, each change in your own behavior is likely to be met by an appropriate change in the organization's behavior. Thus, one reason to be a good design detector is to recognize those systems for which ordinary variations in your behavior are unlikely to produce a different and favorable result for you. Discovery of such an entity will lead either to the design of "extraordinary" variations to deal with the design responses of the other or to breaking off contact.

The reader may now suspect that we are blundering toward a biological theory of mind. Encountering a creature that detects and responds to the intention of a single control system in another creature might not inspire attributions of a theory of mind to the detecting creature. But encountering a creature that detects cues to which of several control systems is active in another creature and responds appropriately might tempt one to the view that the first creature uses a theory of mind to predict the behavior of the other creature. And this would seem to imply that many animals have and use "theories of mind" even if they do not necessarily have "a mind" in which to hold their mind theories (cf. Whitten, 1996).

For the present, the notion of Brentano and others that intentionality is a unique property of human language or the human mind or the human brain has been shown to be false. Every organism or part of an organism that is designed to regulate a variable displays the "object-directedness" (gerichtetsein) of intentionality. This result solves a flock of problems that have bedeviled bio-behavioral analysis. It shows how we may safely deploy attributions of mental activities to other creatures as descriptors of high-order patterns of relation between those creatures and their environments. It distinguishes the mind (the suite of the higher order patterns that characterize a creature's behavior) from the body (the physiological mechanisms that co-ordinate and organize those patterns) without entangling us in endless metaphysical disputations. Finally, it suggests the value of the systematic description of the behavioral organization living creatures—the very program that ethologists and ethnographers once took as their highest calling.

ACKNOWLEDGMENTS

Many people helped us with this manuscript, including Tamer Amin, William Baum, Alex Genov, Peter Killeen, Francois Tonneau, Jaan Valsiner, David Stevens, Jim Laird, and Penny and Caleb Thompson.

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Chapter 9

EVOLUTIONARY MODELS OF MUSIC: FROM SEXUAL SELECTION TO GROUP SELECTION

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ABSTRACT

Ever since the publication of Darwin's *Descent of Man* in 1871, the survival value of music for the individual has been placed into question. Darwin's solution to this problem was to argue that music evolved by sexual selection as a courtship device to increase reproductive success. He envisioned music as functioning analogously to the courtship songs and advertisement calls of many animal species, most of which are performed exclusively by males during a breeding season. However Darwin's thinking predated the comparative study of world music-cultures, which developed only in the late 19th century. The 20th century anthropological study of music has been overwhelmingly group-functionalist in its thinking. Music is almost exclusively described in terms of its manifold roles in supporting group function—with regard to both within-group cooperation and between-group competitiveness. In this essay, I criticize the sexual selection model of music and attempt to channel the group-functionalist thinking of the ethnomusicology literature into a group selection model. Music is a powerful device for promoting group identity, cognition, coordination and catharsis, and it has a host of design features that reflect its strong role in supporting cooperation and synchronization at the group level, features

Perspectives in Ethology, Volume 13: Evolution, Culture, and Behavior
edited by Tonneau and Thompson, Kluwer Academic/Plenum Publishers, New York, 2000

such as the capacity for pitch blending and the use of isometric rhythms. I argue that music and group rituals co-evolved during human evolution such that ritual developed as an information system and music its reinforcement system. Music is a type of social "reward" system, analogous to the neuromodulatory systems of the brain. This view accounts for music's universal association to ritual activities as well as its psychologically rewarding properties.

1. INTRODUCTION: EVOLUTIONARY MUSICOLOGY MEETS SOCIOMUSICOLOGY

Dmitri Shostakovich composed his Seventh Symphony, the "Leningrad" Symphony (Op. 60), in 1941 at the beginning of the nazi siege of Leningrad in a kind of outburst of patriotic spirit. The Symphony quickly became an important international symbol of the resistance of the Russian people to the nazi threat. Personal accounts from the period tribute this symphony with giving both the citizens and soldiers of Leningrad the moral strength necessary to resist the siege. So important was the Symphony to the morale of the people that those front-line soldiers who were also trained musicians were transported from the battlefront to the concert hall to perform the Symphony on live radio at the height of the siege on August 13, 1942 (Wilson, 1994). Shostakovich's next symphony, the Eighth Symphony (Op. 65), was composed two-and-a-half years later, after the 872-day siege of Leningrad had lifted, not as a work of patriotism but as a work of suffering and mourning for both the people of Leningrad and for the nearly 20 million Russians who were to die by the war's end. The work is, through and through, an expression of despair and horror. Interestingly, the Eighth Symphony was condemned at the 1948 meeting of the Communist Party Central Committee for its overly catastrophic vision of the war and for Shostakovich's general use of "formalistic distortions" (Schwarz, 1986).

Although I've chosen examples of European classical music to make a point, this brief description of the history of two of Shostakovich's middle symphonies tells us something about the general features of musics throughout the world. Music is a cultural communication device, and musical performance is often directed and transmitted to the entire social group. Music deals with group strivings, actions, memories, attitudes, and emotions. Group-wide transmission of music has the effect of unifying people spiritually and of coordinating their behavior towards common ends. Music has social meaning, and this meaning comes from both the context of a performance and from the contents or referents of a musical work.

These referents needn't be immediate events, but can allude to past and future events. Thus, music can serve an historiographic function, in terms of the transmission of group history and the marking of important events in the life of the group. Music is as representational as it is directly emotive. And although neither of the Shostakovich symphonies mentioned above makes use of words, music is one of the major vehicles for the transmission of texts (oral and written) and their underlying philosophies and prescriptions, especially in the case of ritual/religious texts. Consequently, verbal song is a universal feature of human cultures.

1.1. Evolutionary Musicology

This chapter is but one of many articles and books which have in recent years attempted to provide an evolutionary perspective on human cultural behavior. In doing so, it brings us face to face with several intellectual traditions in this area, everything from sociobiology (E. O. Wilson, 1975) and evolutionary psychology (Barkow, Cosmides, & Tooby, 1992) to Darwinian anthropology (Boyd & Richerson, 1985; Durham, 1991) and gene-culture co-evolutionary theory (Cavalli-Sforza & Feldman, 1981; Lumsden & Wilson, 1981). Moreover, it brings us in contact with historical theories of music origin, and most especially with the theory of sexual selection, which, since Darwin (1871), has viewed human music in relation to the courtship function served by singing in several animal species.

For a long time I believed that we had only two available reference-frames in thinking about the origins of music: a "singing-animal" model and a "chimpanzee-society" model, where the first makes reference to the role of singing in animal species quite distant from humans and the second looks to species much closer but which lack behaviors that strongly resemble singing or music. One could say that the first model is based on evolutionary analogy and the second on (presumed) homology. Given their reciprocal weaknesses (phylogenetic distance vs. absence of function), the singing-animal and chimpanzee-society models provide complementary ways of thinking about music origins. Be that as it may, is it proper to view human musical capacity as some sort of chimera between the creative vocalization capacities of birds and the social intelligence and group structure of chimpanzees? How much insight do we ultimately gain from such animal models?

I now believe that there has to be a third way of thinking about this issue, one that places humans at both the starting point and end point. This is not to say that there is not invaluable information to be gleaned from studying animal behavior but rather that at some point studying analogous behaviors in genetically-distant species and all-but-absent precursors in

genetically-close species shifts from being a source of enlightenment to being a type of excess baggage that cannot be gotten rid of. At some point we must consider human behavior on its own terms to understand what it is that evolutionary hypotheses need to explain. The point of this argument is not to brush aside the question of precursors of musical capacity but to emphasize that any understanding of the route from bird singing to human singing requires not merely a comparative analysis of auditory and vocal capacities (and the analogies or disanalogies therein) but an acknowledgment of the *horizontal* relationships that exist between musical capacity and other human capacities related to it (Brown, Merker, & Wallin, 2000). If we skirt these relationships, we will miss much that is important about music. Human social behavior, group structure, and cognitive architecture are different from those of other species, and music reflects and reinforces this in important ways. It is here where sociomusicology provides important constraints on models in evolutionary musicology, and where the question of music evolution and that of human evolution in general become intertwined. If music-making is an important component of human social behavior, then it becomes increasingly difficult to separate music from all the rest that we think of as human. This point has particular relevance to the evolution of language (Brown, 2000) and ritual behavior (see below).

There is thus a great need before embarking on evolutionary analyses to understand what music is, how it is implemented at the social level, and how it is instantiated at the neurocognitive level. If not, simple-minded evolutionary scenarios based on presumed adaptive function will be little more than bandwagon effects in the contemporary milieu of imposing Darwinian explanations on anything and everything. It is interesting to note that neural and cognitive evidence suggests that music might be an excellent candidate for a cognitive module (Peretz & Morais, 1993).[1] Music displays the kind of neural and cognitive autonomy that evolutionary psychologists are constantly searching for. Howard Gardner (1983, 1993) has described music as being one of seven types of "intelligence" that characterize human cognition. Therefore, if music could be convincingly shown to be adaptive by evolutionary criteria, it would serve as an excellent model of not only a cognitive module but a cognitive adaptation as well (Miller, 2000).

[1] For all the attention that has been accorded art objects in the study of human evolution, the issue of cognitive autonomy has been all but ignored. Art is simply viewed as a marker for other capacities (mainly language) and not for art itself. In contrast, the case for music as a cognitive module is much stronger despite the absence of musical artefacts prior to the upper Paleolithic. So here we have another interesting trade-off of weaknesses in human evolutionary studies: one function with many artefacts but little neural specificity (the graphic and plastic arts) and another with few artefacts but much evidence for neural specificity and cognitive autonomy (music).

What is music for? It seems clear that no monofunctional explanation of music-making is adequate to account for music's manifold roles in human societies. Consider this short list of musical functions: play, work, courtship, dance, pacifying infants, storytelling, ceremonies, festivals, religious rituals, battle, foraging, communication, propaganda, personal symbol, ethnic and group identity, salesmanship, sleep, meditation, healing, trance, communication with animals, and many others (discussed in Kaemmer, 1993 and Gregory, 1997). However, to people raised in Western society, music seems to be little more than a form of entertainment, something that makes life better but which one can live without. No one ever died from lack of music. In addition, extreme musicality can be counterproductive for individual welfare, as demonstrated by the lives of suffering and destitution of many of the great composers and musicians of the European classical tradition (Mozart, Schubert, Beethoven, and Chopin, to name just a few). Many of them lived unhappy lives plagued by poverty, physical disease, and mental illness. So how could music be adaptive?

Not surprisingly then, the survival value of music has been repeatedly questioned by thinkers both inside and outside of musicology (Darwin, 1871; Granit, 1977; Roederer, 1984; Sloboda, 1985; Jackendoff, 1993; Pinker, 1997). Evolutionists have proposed two solutions to the conundrum of the apparent adaptive-inutility of music. The first one is that music evolved as an elaborate courtship display, similar to several forms of animal song, and therefore that music evolved by sexual selection. The second one is that music's adaptive value lies not at the level of the individual but instead at the level of the group, and that music evolved by group selection. Whether one chooses to think of music in terms of sexual selection or group selection depends, in large part, on whether one views music principally as a competitive or cooperative activity within groups. But, as I will argue below, music is both of these things, and these two perspectives serve as complementary rather than opposing explanations for the evolution of music. Music has features of both a sexually-selected and group-selected trait, and the value in choosing one perspective over the other depends on whether one places the conceptual lens on the individual or the group, in other words, whether one looks at fitness consequences at the within-group level or the between-group level (Dugatkin & Reeve, 1994; Sober & Wilson, 1998).

I will review the arguments for both of these selectionist accounts of music below. But before we rush blindly into a consideration of Darwinian fitness consequences, let us first allow ourselves a broad and cultural view of music, rather than a narrow and selectionist one. Let us consider the full span of possibilities before limiting ourselves to monolithic and simplistic mechanisms that invariably reduce musical diversity to the level of developmental noise.

1.2. Sociomusicology

The quintessential question in the field of sociomusicology is the following: What is the relationship between musical structure and social structure? Such a question has its counterpart in behavioral ecology where study of the "design features" of communication signals in animals is a prime area of concern. In communication, as in morphology, form reflects function, and this is no less true of music than it is of vervet monkey alarm calls, gibbon great calls, and reed warbler territorial songs. An understanding of the relationship between musical structure and social structure requires first and foremost a consideration of how music is employed at the social level. In the most general sense, music acts as an *emotive enhancer* of cultural objects other than itself. It acts to give emotive salience to those things with which it is associated, and it is used for this purpose in a widespread manner in cultures small and large. Music never really stands alone; it is always about other things, always a component of other activities and other meanings. As sociomusicologists have been quick to point out, even where explicit attempts are made to divorce music from its contents and contexts, it is always an embodiment of the social, and much has been made of the fact that seemingly innocuous devices such as intervals, scales and rhythms can be codes for gender, power struggles, moral virtues, universal truths, and the like (reviewed in Martin, 1995).

How is this enhancer role for music manifested at the social level? The most prominent and universal context for the use of music is in so-called ritual situations, that context which is most remote from Western listeners but which is at the very core of social life in tribal cultures. Music operates principally at the level of the social group, rather than at that of the individual or dyad, and functions as a powerful manipulator of mass behavior. Music operates in the context of group rituals to make them emotionally and behaviorally salient for participants. In addition, music's association to language makes the underlying contents of the ritual more meaningful, sacred, and memorable. Thus, music doesn't merely accompany the ritual, it is about the ritual. The result of music's emotive enhancement and semiotic tagging is to allow the members of a social group to enter into a type of contract which is not only musico-linguistic but audiovisual and audiokinetic as well, and it is this collective contract that permits the many functions of music mentioned above. For this to occur, it is not important that all members of the group perform together. A pop concert involving a single musician and 20,000 spectators is best seen in terms of the emotional synchrony (and often kinetic synchrony) that characterizes the experience. To the extent that this is so, we see an important contrast to the typical social arrangement of speech. Speech tends to act at the dyadic level to influence behavior inter-individually, and its grammar is designed to express

behavioral relationships between individuals (i.e., who did what to whom). Music invariably acts at the group level to influence mass behavior and, as I will describe later on in the chapter, it has several design features that make it ideally suited to do exactly this.

The operative metaphor here is not "display," the one that ethologists are so fond of attaching to song, but "communication." Music is a group-level communication system whose sound-devices and meanings are socially structured and socially exploited. Music's involvement in group rituals makes it an ideal device for coordinating behavior, reinforcing norms, transmitting history, and synchronizing emotions in ways that lead to collective and cooperative action. As Alan Lomax (1980) has written: "A musical performance is an enactment in public of a synchronic plan which shapes the interaction of culture members in the everyday survival activities that constitute the culture. Musical performances (. . .) reinforce the strategic models by means of which and in terms of which cultures endure" (p. 57). The real question, though, is how music does this. What is the relationship between the sound properties of music in a given culture and "the strategic models by means of which and in terms of which cultures endure"?

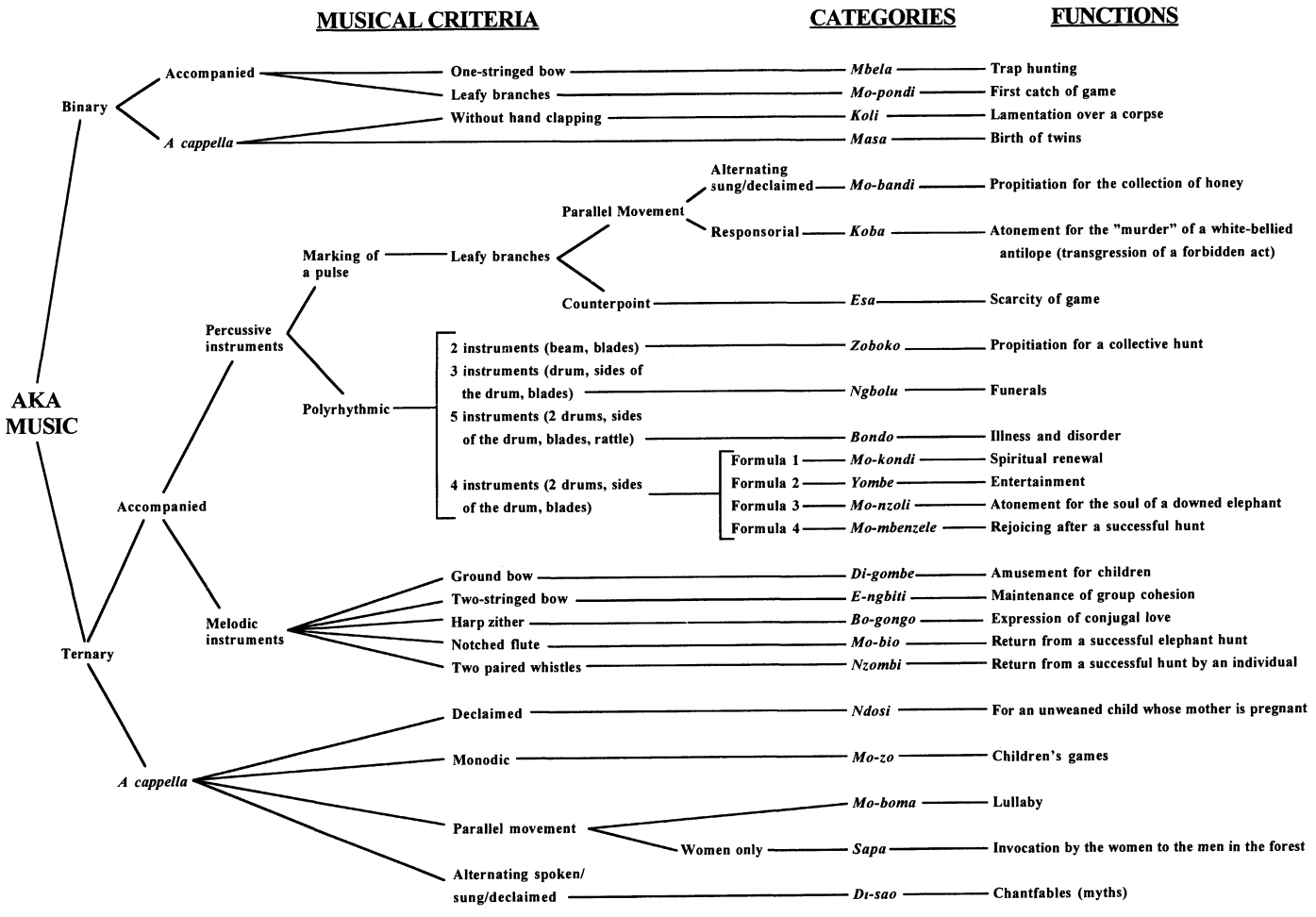
This is clearly a complex question, and we can only provide a glimpse of the answer here. A study by Arom and Khalfa (1998) of the musical forms and associated social functions of the Aka Pygmies of central Africa gives us some idea as to how such an analysis might proceed. Arom began studying the music culture of this population in the 1960's and devised a systematic analysis of its music (Arom, 1991). As shown in Figure 1, Arom and Khalfa identify about two dozen musical categories (forms) in this culture, which "in the current state of our knowledge represents the complete system of categories of Aka music" (p. 13, my translation). Although it is premature to conclude that this profile is representative of all hunter-gatherer music cultures, Arom's is the most comprehensive analysis to date, and so we should view it as an adequate model of such a culture until further studies lead us to believe otherwise.

Arom and Khalfa (1998) describe three interesting features of Aka music culture. First, musical forms occur as discrete categories, and the complete repertoire of Aka music can be seen as the sum of these categories. Second, each category is strictly linked to a particular social function and thus performance context. No musical form is performed outside of its appropriate context, and each context strictly demands performance of a given musical form. This is what ethnomusicologists refer to as "functionality", and is known to apply to virtually all tribal cultures. Third, each category has a distinguishable set of musical parameters and performance arrangements that characterize it. As Arom and Khalfa describe it, each musical form is distinguishable from any other by at least one musical property, be it at the level of rhythm, scale, instrument type, performance

ensemble, and so on (Figure 1). These musical parameters and arrangements are instantly recognizable to all members of the group, thus making each category of musical form distinguishable on a purely acoustic basis. Putting this together, we see that each social category is related to musical structure in a distinct fashion: "Each category is indissociably linked to a function or determinate social circumstance, which is attested to by the fact that the name it has in the vernacular language is, without exception, the same as the function in question. But, and this is the crucial fact, each of these categories is *musically determined*: there is no category which is not distinguished from all the others by at least one musical property" (p. 15, my translation, emphasis in original). What this analysis highlights is that at the level of hunter-gatherer populations, musical structure is strictly and determinately related to social function in a manner which is consensually recognized.

What can we conclude from the discussion of this section? If the functionality that Arom and Khalfa describe implies that a particular social context requires the performance of one music and not another, then we can safely conclude that performance of the appropriate music is essential for performing the social activity to begin with. In hunter-gatherer populations like the Aka Pygmies, music is an essential component of literally all social activities, and it does not require a great stretch of the imagination to believe that the same must have been true of our hominid ancestors. Music reinforces "the strategic models by means of which and in terms of which cultures endure." How music does this can be understood at several different levels. At the affective and motivational levels, music is a type of emotive enhancer, and to the extent that music is experienced in a group fashion during ritual events, this enhancement promotes the synchronization of group emotion, motivation, and action. But it is wrong to see music as a purely limbic or hedonic function, as it is always an embodiment of the social: its forms and structures reflect underlying social relationships and structures. In hunter-gatherer societies, musical form is strictly linked to

Figure 1. The Musical Forms of the Aka Pygmies. This table provides a complete description of the musical repertoire of a hunter-gatherer culture—the Aka Pygmies—as outlined by Arom and Khalfa (1998). The column labeled "categories" provides the name of each musical form in the vernacular language of the Aka people. This name corresponds exactly to the social activity accompanied by each musical form, as shown in the far left column labeled "functions". The rest of the table shows how each form is musically distinguishable from all others by at least one musical criterion, resulting in a correspondence map between musical structure and social function. This figure is a direct translation from the French by the author and is printed with the permission of Simha Arom and the *Revue de Musicologie.*


MUSICAL CRITERIA
CATEGORIES
FUNCTIONS
AKA MUSIC
Binary
Accompanied
One-stringed bow
Mbela
Trap hunting
Leafy branches
Mo-pondi
First catch of game
A cappella
Without hand clapping
Koli
Lamentation over a corpse
Masa
Birth of twins
Ternary
Accompanied
Percussive instruments
Marking of a pulse
Leafy branches
Parallel Movement
Alternating sung/declaimed
Mo-bandi
Propitiation for the collection of honey
Responsorial
Koba
Atonement for the "murder" of a white-bellied antilope (transgression of a forbidden act)
Counterpoint
Esa
Scarcity of game
Polyrhythmic
2 instruments (beam, blades)
Zoboko
Propitiation for a collective hunt
3 instruments (drum, sides of the drum, blades)
Ngbolu
Funerals
5 instruments (2 drums, sides of the drum, blades, rattle)
Bondo
Illness and disorder
4 instruments (2 drums, sides of the drum, blades)
Formula 1
Mo-kondi
Spiritual renewal
Formula 2
Yombe
Entertainment
Formula 3
Mo-nzoli
Atonement for the soul of a downed elephant
Formula 4
Mo-mbenzele
Rejoicing after a successful hunt
Melodic instruments
Ground bow
Di-gombe
Amusement for children
Two-stringed bow
E-ngbiti
Maintenance of group cohesion
Harp zither
Bo-gongo
Expression of conjugal love
Notched flute
Mo-bio
Return from a successful elephant hunt
Two paired whistles
Nzombi
Return from a successful hunt by an individual
A cappella
Declaimed
Ndosi
For an unweaned child whose mother is pregnant
Monodic
Mo-zo
Children's games
Parallel movement
Mo-boma
Lullaby
Women only
Sapa
Invocation by the women to the men in the forest
Alternating spoken/ sung/declaimed
Di-sao
Chantfables (myths)

social function, and therefore music plays a critical role in defining just what those social functions are.[2]

The following sections of this chapter will analyze the two major types of selectionist scenarios that have been proposed to account for the existence of human music. From the above discussion, it should be clear that music is not merely a vocalization system or a display behavior but a communicative and semiotic device of great richness and flexibility, whose functions, meanings, and uses are socially derived and socially controlled. Selectionist scenarios that ignore this can only be expected to provide the most incomplete account of the origins of music.

2. SEXUAL SELECTION AND MUSIC: MUSIC-MAKING AS A COURTSHIP DISPLAY

Sexual selection is a mechanism of natural selection that considers the consequences of a trait for mating success rather than individual survival. Traits that are sexually selected work in the service of competition and selection for mates, even though they may have no other type of survival function, and may even work against survival. Sexual selection of a trait can be defined as "differences in reproductive success caused by competition over mates and related to expression of that trait" (Andersson, 1994, p. 7). The theory of sexual selection was developed to explain sexually dimorphic traits, especially exaggerated (usually male) traits that seem dysfunctional from the standpoint of individual survival. It was first elaborated in detail by Charles Darwin in *The Descent of Man, and Selection in Relation to Sex* (1871).

2.1. Sexual Selection Theory

Sexually selected traits generally assume one of two forms: weapons and ornaments. The former are mainly involved in intrasexual competition

[2] Two questions that are critical for understanding the form-function relationship in music, but which I have no room to discuss, are the following: 1) Given that each social function is associated with a particular set of musical properties in hunter-gatherer populations, what is the relationship between a given social function and its musical properties? In other words, assuming that this relationship is not an arbitrary one, why are particular musical properties associated with certain social functions and not with others? 2) The next question is how this relationship occurs at a cross-cultural level. Are there universal trends relating musical properties to social function? In addition, how does music reflect not just social function but social *structure* and its underlying personal relationships and power hierarchies in different cultures? Lomax (1968) has performed a global analysis of this issue, and some of his results are presented in later sections of this chapter.

(usually inter-male conflict), and consist of such things as horns and sharp teeth. The latter, by contrast, are involved in intersexual advertisement, and consist of exaggerated secondary sexual traits such as bright plumage or elaborate courtship displays. Because weapons are often explainable in terms of natural selection due to their utility for individual survival, the task for sexual selection theory is to explain physical and behavioral ornaments. Two sexual-selection mechanisms have been invoked to explain the evolution of ornaments: runaway processes and indicator mechanisms (Andersson, 1994). The first involves a positive feedback cycle between a male's ability to develop a secondary sexual trait and a female's preference for an even more exaggerated form of it. The second considers ornaments as signals of health, fitness, and good genes, and assumes that such traits evolve because they are favored by females who use them in selecting males of good quality. As these features are often disadvantageous to survival, they are said to be "handicaps" which serve as honest signals of fitness (Zahavi, 1975).

Much of the sexual selection literature focuses on male displays and female recipients, where such displays are produced by either single males or groups of competing males (i.e., leks). However, in some species the female is the dominant one in courtship and territorial matters, and thus sexual selection in these cases applies to female traits and male recipients.

2.2. Darwin (1871)

Darwin brilliantly laid down the foundations for virtually all the modern-day concepts of sexual selection. But he was also interested in extending his analysis, based almost exclusively on animals, to humans by showing that sexual selection could explain courtship behavior and other traits in humans. One thing that he mentioned in this regard was music. While scientific theories of music origin in the West date back to the 18th century (Thomas, 1995), and while there are no doubt countless tribal myths about the origins of music, the first biological theory of music origins was Darwin's, as expounded in 10 pages of the second part of *The Descent of Man, and Selection in Relation to Sex* (1871).

Like many others after him, Darwin questioned the utility of music for individual survival: "As neither the enjoyment nor the capacity of producing musical notes are faculties of the least direct use to man in reference to his ordinary habits in life, they must be ranked amongst the most mysterious with which he is endowed" (p. 335). And so he proposed that music evolved by sexual selection as a form of courtship behavior akin to the vocal courtship displays of insects, frogs, and birds. Darwin pointed out that many of these vocalizations were performed exclusively by the male

of the species, and tended to be expressed primarily during the breeding season. His basic hypothesis was that music too evolved as a means of "charming the opposite sex." However, Darwin was much less clear about who was doing the charming: "We have hardly any means of judging whether the habit of singing was first acquired by the male or female progenitors of mankind" (p. 337). Of course, sexual selection could in theory accommodate either possibility.

In reality, despite his strong ground in talking about the courtship role of song in many animal species, Darwin ultimately made a very weak case for sexual selection in music, as he openly acknowledged that little to nothing was known about courtship calls in mammals, the exception being the gibbon, whose complex song Darwin mistakenly took for a seasonal courtship call (see below). While he states in a footnote that "musical notes and rhythm were first acquired by the male or female progenitors of mankind for the sake of charming the opposite sex" (p. 336n), he bases this hypothesis on little more than the analogous singing behavior of other animals rather than on any kind of direct ethnographic evidence that music is indeed involved in human courtship. In other words, Darwin relied exclusively on evolutionary analogy in making his case for sexual selection in music.

Darwin's theory of music, while far from being the centerpiece of his sexual selection theory, was the first attempt to explain music's aesthetic properties in adaptive terms. It was the first biological explanation for why music should be creative and elaborate and attention-grabbing and emotively affecting and physically challenging. Unfortunately, Darwin's analysis of music did not stimulate any type of response or following in either biology or musicology until quite recently.

2.3. Miller (2000)

Geoffrey Miller (2000) presented the first detailed sexual selection account of music since Darwin. In addition to providing a strong and clear statement of the sexual selection perspective as applied to music, Miller plotted out with utmost clarity the adaptationist program for music. In this regard Miller's essay is required reading not only for those interested in the evolutionary psychology of music but for anyone interested in the evolution of human cultural behavior generally. Unlike Darwin, Miller makes a strong case for sexual selection in human music and does so with the tools of both modern sexual selection theory and evolutionary psychology. I will take the liberty of summarizing Miller's essay in the form of four principal arguments.

1. *Music is costly but provides no individual survival benefits.* Like Darwin before him, Miller points out the general conundrum of the survival value of music. Music can be seen to involve several types of individual costs in terms of time, energy, motor skills, training, cognitive abilities, and so on. Miller points out that music and dance rituals in tribal cultures can last not only through the night but for several days. This requires not only a great investment in time but severe physical endurance as well. Like Darwin before him, Miller argues that the individual fitness costs involved in music-making are made up by the reproductive benefits that accrue to men who sing and dance for prospective mates. "Music is a complex adaptation, and it has costs, but no identifiable survival benefits. Therefore, it is most likely to have evolved due to its reproductive benefits" (p. 337).

2. *Most complex acoustic signals in nature are used in courtship. Music is analogous to them.* Like Darwin, Miller points out that music-making, as an acoustic behavior, is analogous to many forms of courtship call and song in animal species: "Bird song and human music do not share a common phylogenetic origin, but they may very well share a common adaptive function" (p. 355). But he makes this claim much broader: "Given that almost all complex acoustic signals produced by other species are courtship displays, [then] this courtship hypothesis for human music is not only better supported by music's design features, but should be considered the evolutionary null hypothesis" (p. 329).

3. *Music and dance function as both aesthetic displays and fitness indicators in the service of human mate choice.* Up to this point, Miller's account closely follows Darwin's. But then Miller develops a detailed hypothesis of how music-making could satisfy the criteria of a sexual selection model. He argues that music and dance function as both fitness indicators and aesthetic displays. With regard to the former, we can imagine music and dance serving as indicators of aerobic fitness, physical endurance, and motor coordination, as well as cognitive indicators of learning, memory, auditory function, linguistic skill, creativity, and the like. At the level of aesthetic display, one could point to the aesthetic appeal of the singing voice, the elaborateness of improvisational music and dance forms, and the myriad opportunities that dancing affords to show off the form and function of the human body. Although Miller does not cite any ethnographic evidence for the direct use of music in human courtship, he gives a list of criteria for testing an evolutionary

psychological hypothesis that music is in fact a device for impressing and stimulating the opposite sex for courtship purposes.

4. *Musical behavior throughout the life span is consistent with a sexual selection hypothesis.* Finally, Miller argues that the ontogenetic pattern of human musical expression is consistent with the expression of any sexually selected behavioral trait. He argues that music is preferentially performed by men of reproductive age and that an individual's musical activity declines after this time. "Over the life span, public music production rockets upward after puberty, reaches its peak in young adulthood during the period of most intense courtship, and declines gradually with age and parenting demands" (p. 337).

In sum, Miller revives Darwin's 1871 hypothesis that music evolved for courtship purposes but brings it into the modern age. Whereas Darwin was noncommittal about which sex was charming the other, Miller explicitly states that human music has the form of most courtship vocalizations in other animals where it is the male who does the singing. Music is not only an aesthetic display but a good indicator of male quality. Miller argues that this courtship hypothesis is supported by ontogenetic data and by evolutionary psychological considerations about the effects of music on the two sexes.

2.4. Problems with the Sexual Selection Argument

I see many problems with a sexual selection account of music. For one thing, it sees music as a purely competitive activity in which men compete with one another for the affinities of women. It allows little room for music as a cooperative activity within groups. In addition, both Darwin and Miller make weak social cases for music. Music is little more than a bird display, and it is difficult to reconcile this with the major sociological issues that are raised in current theorizing about uses and control of music (Martin, 1995; Brown & Volgsten, in preparation). I shall present a critique of the sexual selection hypothesis of music in the same form as it was presented above.

1. *Music is costly but provides no individual survival benefits.* I will defer this issue to the next section of the chapter, and merely mention here that if music-making were a group-selected cooperative display, this would account for many of the same elaborate and seemingly-functionless features of music that sexual selectionists highlight in their arguments. In fact, it would probably explain quite a bit more about the actual acoustic features and performance properties of music.

2. *Most complex acoustic signals in nature are used in courtship. Music is analogous to them.* If, like Darwin and Miller, we employ an approach based on evolutionary analogy, then we see that not only are all complex acoustic signals in animals *not* involved in courtship, but that *the most complex signals are not used primarily in courtship*. Unlike the highly monotonous and repetitive courtship signals of cicadas, frogs, and many species of birds, the most acoustically-complex vocalization signals in nature come from the monogamous singing species, such as gibbons and several species of tropical birds, who sing elaborate duets. As in music, increases in the size of the performance ensemble can greatly increase the acoustic complexity of the signal.

As mentioned above, Darwin based part of his reasoning for sexual selection in mammals on the singing of the gibbons, and he incorrectly attributed a seasonal courtship function to it. By all contemporary accounts, gibbon duetting functions in the maintenance of year-round territories and the strengthening of pair bonds in already-formed monogamous couples (reviewed in Geissmann, 2000). There is little to no evidence that unpaired males sing to attract females (Mitani, 1988). The same is true of several species of monogamous birds that live in the tropics which, like gibbons, use duetting to defend year-round territories (Farabaugh, 1982).

There are several features of duetting that bear an important resemblance to human music which cannot be accounted for by a courtship hypothesis of music. 1) Certain features of music, such as responsorial, antiphonal, polyphonic and homophonic singing, are only conceivable when discussing coordinated, multi-singer performance and not solo singing or even singing in leks. Multi-singer coordination greatly increases the potential complexity of acoustic signals. It permits what in the human sphere is called "multi-part music." 2) Biologically, both sexes are singers. In addition, both sexes make more or less equivalent contributions to the song, in contrast to the asymmetry of male singers and female recipients found in courtship songs and advertisement calls. In the case of gibbons, it is usually the female that makes the more dominant and more elaborate contribution to the song with the male (of many species) singing both an introduction and a coda to her "great call" sequence (Haimoff, 1984). Thus, while the male and female contributions to the gibbon duet are sexually dimorphic, the capacity to sing is not. In the case of humans, lack of asymmetry is even more extreme, as women are just as capable as men of performing musically. Music is not a sexually dimorphic trait in humans. 3) Duetting

is cooperative and coordinated, rather than competitive or disjoint. Gibbon couples place a high premium on maintaining tight coordination, and will terminate and restart a duet if the appropriate level of coordination is not achieved (Haimoff, 1984). Duetting is not a contest but a display of cooperative strength. 4) Duetting is involved in defending year-round territories (Leighton, 1986), just as in many human tribes and bands. Daily duetting is a highly ritualized "keep out" signal accompanied by exaggerated physical displays. Whereas the males of many bird species terminate singing behavior after finding a mate (e.g., Catchpole, 1973), monogamous species such as gibbons sing all year round and throughout their lifetimes in defense of year-round territories. 5) Duetting, like human music, is thought to play a significant role not only in defending territories but in maintaining social bonds. Such a function is not restricted to duet singing among monogamous species but is found quite prominently in the social calls of many primate species (Ujhelyi, 2000). While such calls do not have the acoustic complexity or coordination of the duets of the monogamous species, they foster group identity and social bonding in a manner similar to them and to music (Geissmann, 2000). It is important to point out that none of the known primate calls in thought to be directly involved in courtship. Primates do not seem to exploit vocalization for courtship purposes, but instead rely on visual, olfactory and kinetic cues. Courtship calls are rare to nonexistent in hominoids, whereas territorial calls are ancestral to the entire group of species. Therefore, territorial calls, rather than courtship calls, are far and away the most likely hominoid precursor for human music (Geissmann, 2000).

Perhaps the biggest disanalogy between humans and the duetting species with regard to singing is that humans are a highly social, group-living species that live in tight-knit, cooperative groups, and that their musical expression tends to occur at the group level (rather than at the couple or family levels), involving groupwide integration of sound and movement. The important lesson that emerges from this study of evolutionary analogy is that form reflects function: just as solo singing is important for attracting mates and defending individual territories, and duetting is important for a maintaining a couple's territory and solidifying the pair bond, then group singing among humans most likely functions in the maintenance of group territories and the strengthening of group identity and cohesion.

In sum, many complex animal vocalizations have evolved that bear no direct relationship to courtship. Part of their complexity

comes about simply by the use of multi-part performance, as in music. Importantly, musical capacity is not a sexually dimorphic trait and this greatly weakens claims that music evolved by sexual selection as a device for men to court women. It is most likely that human singing evolved as a group territorial and cohesion device analogous to singing in duetting species and social calling in many primate species.

3. *Music and dance function as both aesthetic displays and fitness indicators in the service of human mate choice.* The potential of music and dance to function as aesthetic displays and fitness indicators is, to my mind, both the strongest and weakest part of the sexual selection argument for music. On the one hand, it seems quite convincing that the sensory, motor, cognitive, and energetic skills involved in music-making could be excellent indicators of fitness, both male and female. In addition, things like vocal quality, creativity, and style of movement could be quite useful as aesthetic displays in situations that involve music and dance performance. However, at the same time, I see a critical problem with this reasoning, one which Miller indirectly acknowledges: "Sexual selection through mate choice is almost unfairly powerful as an evolutionary explanation for things like music that seem impressive and attractive to us, but that seem useless for survival under ancestral conditions. The reason is that any feature one is even capable of noticing about somebody else (including the most subtle details of their musical genius) could have been sexually selected by our ancestors" (Miller, 2000, p. 355). To my mind, there is something worrisome in this reasoning because it is so all-encompassing. Any feature one is capable of noticing about somebody is a feature that could have been sexually selected. This kind of argument just sucks all the specificity out of music because, at some level, *any* behavior could be reduced to these terms. The display role emphasized by sexual selectionists is so obvious and unavoidable as to be irrefutable. Some form of display, voluntary or involuntary, occurs in all public behavior. A display hypothesis explains little about music's melodic and rhythmic systems.

   Another way in which a sexual display hypothesis of music becomes highly problematic is that it has a strong tendency to conflate music and dance. There is a fine line to be drawn here. On the one hand we want to emphasize the important historical roots and contemporary links between music and dance, but on the other hand, we need to emphasize that music and dance are very different systems, based on different organizing principles, although they have important connections at the levels of rhythm and phrasing.

It is much easier to see dance as a type of display, but at the same time it is much easier to see it as an extension of generalized motor capacities. Dance satisfies few of the criteria of specificity that we would expect of a behavioral adaptation. Music, in contrast, has many features of cognitive autonomy and specificity. If the goal of this exercise it to explain the evolution of music *qua* music, then we have to start thinking about music itself and not conflate it with dance or dance music. The more deeply we look at music—its syntax, its neural basis, its sociocultural functions and uses—the more inconceivable it is that music can be reduced to "any feature one is capable of noticing about somebody".

Regarding dance itself, we must bear in mind that dance—whether performed solo or in groups—serves a multitude of functions pertaining to ritual re-enactment and social coordination that have no direct relationship to mate choice. In *Keeping Together in Time* (1995), William McNeill recounts, from a broad historical perspective, the importance of the interpersonal synchrony evoked by dance and drill for all types of group functions, from religious rites, to military training, to social bonding. Anthropological analyses of dance (Hanna, 1979; Zemp, 1999) focus as much on gestural representation and social symbolism as on gross movement; dance, like any expressive gesture system, conveys meanings and emotions. As Judith Hanna (1979, pp. 4–5) has written: "Dance is *communicative* behavior—a 'text in motion'—or 'body language' (. . .) Movements in dance become standardized and patterned symbols, and members of a society may understand that these symbols are intended to represent experiences in the external and psychic world (. . .) Dance is a conceptual natural language with intrinsic and extrinsic meanings, a system of physical movements and interrelated rules guiding performance in different social situations" (emphasis in original). Several theories of the origin of language propose that gesture preceded vocalization as a device for conveying symbolic meaning (Corballis, 1991; Armstrong, Stokoe, & Wilcox, 1995). We should be skeptical of theories of the origin of dance that do anything less than account for its important roles in gestural symbolism and interpersonal coordination.

In sum, sexual display is but one area where music-making—often in combination with dance—has found an important role in human cultures. However, it is difficult to see courtship as the *raison d'être* of music. Once music evolved, it was cooptable in the form of sexual displays, even highly competitive ones, but I doubt

that this was the initial driving force for the evolution of music's melodic and rhythmic systems. There are much better explanations for music's design features, as will be described below.

4. *Musical behavior throughout the life span is consistent with a sexual selection hypothesis.* This is the point that is most dependent upon human empirical evidence. Miller doesn't present any except as it pertains to recording stars in Western culture. There are two major problems here, one ontogenetic and one ethnographic. The ontogenetic point is clear. The theory of sexual selection was developed by Darwin to explain sexually-dimorphic traits in animal species, arguing that such traits evolved to serve a role in mate selection either directly or indirectly. But, as pointed out above, music is not a sexually dimorphic trait in humans; with the exception of the differing frequency ranges of the voice, both sexes have the equivalent capacity to make music. This in itself should be seen as a critical flaw in the sexual selection theory of music, especially in light of Miller's strong claim that musical production is the principal domain of men. In this regard, territorial singing by gibbons couples provides a vastly superior model of human musicality than does courtship singing in birds and other species.

   This leads to the second major problem with the sexual selection perspective: the absence of any direct role of music in human courtship. If music's courtship function is really something more than a nonspecific feature one is capable of noticing about somebody, then it should have a clear and defined role in human courtship rituals, and not merely an indirect one that is secondary to the process of group assembly. Neither Darwin nor Miler gives empirical evidence for this kind of primary role of music-making in human courtship. Despite the images of romantic love scenes from the American musicals of the 1940's, men simply do not sing to women in a dyadic fashion during courtship rituals as, for examples, some birds do. One of the most frequently perpetuated myths about the musics of tribal cultures is that romantic love songs form a substantial component of their repertoires. Nothing could be further from the truth. Romantic love songs are prominent features only of large cultures. Look again at the musical categories described for the Aka Pygmies by Arom and Khalfa (Figure 1). Only one of two dozen musical categories is about conjugal love, and most of the rest are about the business of collective survival. So the context is imagined to shift to the level of the group where courtship displays assume the role of indicators and aesthetic displays. But then two major problems of interpretation emerge. First,

the group activity at hand usually has *a completely different* underlying function than courtship itself. We are not talking about teen discotheques here; we are talking about the important business of group survival. The contexts surrounding the two dozen musical forms of Aka culture are not simply empty social vehicles for sexual display. Instead, they are critical group functions that form the basis for the stated purpose of the musical activity being engaged in. And as Arom and Khalfa point out, the name for a given musical form in the Aka language is always identical with its social function. Second, human courtship has many other routes for expression, and musical performance is not a major one of them in any culture. Most of human courtship is based on dyadic, face-to-face interactions—rarely, if ever, involving musical performance—rather than on group displays. Music's role in courtship is, at best, indirect. Courtship and marriage are certainly matters of collective importance, and so we shouldn't be surprised that music plays a role in these functions. However, ethnographic evidence argues strongly against the idea that music evolved to serve a direct and primary role in human courtship.

Miller's empirical argument rests on his appeal to the fact that most jazz, rock, and classical recording artists of the last 30 years were men of peak reproductive age. I think that it is safe to say that even if extreme musical talent were genetically heritable (and there is still no evidence to date that it is; see Howe, Davidson, & Sloboda, 1998), all great musicians and composers of all time would have made a negligible contribution to the human gene pool. Clearly what we want to explain is not some extreme talent but a general human capacity. People at any extreme in human behavior are maladapted, and one only has to glance at the life stories of the great European classical composers to know that this is so, not to mention a large number of the people from Miller's list of recording stars. Furthermore, a sex bias at the level of popular music is too easily confounded with cultural factors related to sexual constraints. Such a bias applies perfectly well to book writing, poetry, painting, sculpting, film making, and in fact most important professions in large-scale cultures. It is very difficult to weed out what is a male-specific, sexually-selected genetic capacity from what is generalized male hegemony in most domains of culture. I believe that we must take as our null hypothesis the biological equivalence of the two sexes with regard to musical capacity until convincing functional evidence suggests otherwise.

In summary, while music can certainly be used in courtship contexts, there is little evidence that it plays any direct role in this function. The most

one can say about sexual selection is that music has some potential to serve indirectly as a type of fitness indicator or aesthetic display. This is a far cry from the directness of the social arrangement of courtship singing and advertisement calling in birds, frogs, and cicadas. In its current form, the sexual selection hypothesis lacks specificity about music's design features. Finally, musical capacity is not a sexually dimorphic trait in humans, and in accordance with this, there is little evidence that it is directly involved in courtship. Thus, with regard to the evolution of music, it is most likely that sexual selection has functioned as a form of *indirect selection* operating secondarily to some other more direct selection mechanism. This indirect role is well accounted for by a description of music as some feature that one is capable of noticing about somebody else.

3. GROUP SELECTION AND MUSIC: MUSIC-MAKING AS A COOPERATIVE ACTIVITY

> *"If there are (. . .) adaptations of obvious group benefit which cannot be explained on the basis of genic selection, it must be conceded that group selection has been operative and important."*
>
> G. S. Williams, *Adaptation and Natural Selection* (1966)

Music does indeed have important features that can be illuminated by a sexual selection perspective, most especially its potential to be used as an aesthetic display and fitness indicator. However, I do believe that this is a highly incomplete view, and I think any musicologist unconcerned by the constraints of evolutionary reasoning would immediately come to the same conclusion. What is missing from such a view? So much: music as a group-wide activity; music as a cooperative activity; music as a social communication system; music as a semiotic system; music as a reflector and reinforcer of social structure; music as a socially-valued, socially-exploited, and socially-controlled device. However, Miller (2000) warns us that any group-functionalist account of music-making puts us in the "embarrassing position" of invoking group selection. He provides us with the important caveat that we should not conflate activities that are done *in* groups with activities that are done *for* groups. Strong evidence for group participation is not a sufficient basis for making a case for a group adaptation, as group participation alone does not imply any fitness consequences for the group or its members. Thus, as Miller correctly points out, the onus on a group selection account of music is to demonstrate that music is in fact done *for* groups.

3.1. Background to a Group Selection Model for Music

Before venturing in that direction, it will be necessary to say a few words about multilevel selection and group-level adaptations. This issue is

complicated and multifaceted, and only the most general description of it can be provided here. I believe that music is an excellent test-case for models of group selection in human evolutionary studies, one that could be used to analyze other types of behaviors, especially those that fit into the category of group-ritual behaviors. However, as I will argue at the end of this chapter, the group selection and sexual selection viewpoints will ultimately have to be integrated with one another in order to provide a balanced view of music evolution. This section will present the background to a group-selection model for music, which itself is presented in the following section.

3.1.1. Multilevel Selection Is a Fact of Biology

Group selection is a form of natural selection that involves the differential reproduction of groups, and is classified within the context of multilevel selection. Multilevel selection theory is predicated on the idea that natural selection can act at multiple levels in the biological hierarchy, and thus that adaptations can occur at any of these levels. What this implies is that "vehicles" for natural selection can be found at any level in the biological hierarchy, from genes to communities (Wilson & Sober, 1994). Multilevel selection is a fact of biology; it is simply beyond dispute at this point. The evidence for it ranges from genic selection (Dawkins, 1976), to cell-line selection (Buss, 1987), to individual selection (Williams, 1966), to group selection (Wade, 1978; Sober & Wilson, 1998) and beyond. Multilevel selection has been invoked repeatedly in explaining the origins of biological organization, everything from self-replicating molecules to complex animal societies (Buss, 1987; Maynard Smith & Szathmáry, 1995). The evolution of higher-level biological organization is explained in terms a transition process in which lower-level units coalesce into higher-order structures through a process involving the suppression of individual-level competition and the emergence of cooperative interactions (Maynard Smith & Szathmáry, 1995; Michod, 1997). The fact that the same type of coalescing process occurs at the molecular level, cellular level, tissue level, and organism level is strong support for multilevel selection, and provides a more general and universal perspective on how natural selection operates. It also provides us with the insight that all biological structures are, in reality, a balancing act between the competition and cooperation of their component parts (e.g., cells in tissues).

While multilevel selection is part of the working tool kit of those interested in the evolution of biological organization, the notion that natural selection can act at the level of the group, a possibility inherent in any multilevel perspective, has been fiercely rejected by the establishment in evolutionary biology since the 1960's (Williams, 1966). I will not recount here a history that has been told many times now (Wilson & Sober, 1994;

Dugatkin & Reeve, 1994; Sober & Wilson, 1998) except to point out that the wrath has been unwarranted. An old school of group selection from the 1960's, one devoid of mathematical foundations (Wynne-Edwards, 1962), was replaced by a new school of group selection in the 1970's that was based on the quantitative principles of natural selection. The latter took the form of "trait-group" models, as developed by David Sloan Wilson (1975, 1980; see also Price, 1970, 1972; Hamilton, 1975). One important feature of such models is that they partition the variance of fitness into within-group and between-group components. When there is no group component to fitness, these models reduce to classical models of individual selection. However, when there are group effects, such models are capable of detecting them. The best-described group effect in the evolutionary literature is the one involving family members, an effect known as kin selection (Hamilton, 1963, 1964; Maynard Smith, 1964). A controversy has been raging since the 1970's as to whether the fitness function of kin selection should be described as a group component to a compound fitness function (as per trait-group models) or as an extended component of individual fitness (as per kin selection models). However, several theoreticians have now conceded that "the mathematics of the gene-, individual-, kin- and new group-selection approaches are equivalent (. . .) Individual and trait-group selection are not alternative evolutionary mechanisms; rather they are alternative pictures of the same underlying mechanism" (Dugatkin & Reeve, 1994, p. 108).

While it may be true that individual- and group-selection models provide alternative pictures of the same mechanism, it is decidedly not the case that the two pictures provide the same information. The best reason I can think of for getting involved in this vociferous levels-of-selection debate is that hierarchical approaches to natural selection provide a hands-down advantage over nonhierarchical approaches in that they allow one to distinguish causal factors *at the level at which they act* (Dugatkin & Reeve, 1994). In the same way that one doesn't analyze selfish genes (i.e., selfish DNA) and intragenomic conflict in terms of individual selection, then there are many phenomena that are only explainable as group-level effects. One can probably stretch the concept of individual fitness *ad infinitum* to accommodate any group-level effect, but in many cases this will only deprive one of powerful insights into the causal structure of the phenomenon in question. Natural selection is an intrinsically hierarchical process.

3.1.2. Groupishness Is a Missing Concept in Evolutionary Psychology

Much of the discussion of group selection in the evolutionary literature has focused monolithically on the question of altruism (Sober & Wilson, 1998), in other words on behaviors that are individually costly but beneficial to others. However, I would like to suggest that the central issue

of group selection, especially for human evolutionary studies, is not altruism but a concept that I will call *groupishness*, which refers to a suite of traits that favor the formation of coalitions, promote cooperative behaviors toward group members, and create the potential for hostility towards those outside the group. Altruism is but one component of this suite. Groupishness is similar in several important respects to the "syndrome of ethnocentrism" described by LeVine and Campbell (1972). Group selection theories have been naively criticized as feel-good theories of selfless cooperation, but the concept of groupishness highlights the fact that any such feelings are completely ambivalent, that the positive and negative go hand in hand in a truly binary fashion. A large social psychological literature supports the idea that while positive feelings and cooperative behaviors are extended towards members within the group, negative feelings and hostile behaviors are shown towards those outside of the group (see below). To see group selection exclusively in terms of ingroup cohesion ignores an essential facet of human psychology that goes together with cohesion. However, to see it exclusively in terms of warfare and forced extinction is to miss the important point that cooperation allows groups to function as adaptive entities even in the absence of direct inter-group conflict. As Christopher Boehm (1997) has pointed out, many of the most important selection pressures that affect the survival of human groups are environmental, factors such as climate, predators, parasites, and the like. Therefore, traits that make groups better functioning are very often poised to make them outsurvive groups that function poorly without there ever being direct conflict between them.

Groupishness is one of the most important concepts missing from the evolutionary psychology approach to human behavior (Barkow, Cosmides, & Tooby, 1992). It is not simply about the human tendency to spontaneously form coalitions and alliances but about a complex set of emotions, attitudes, and motivations that support the human inclination to live in groups and form life-long attachments to people, qualities that make human societies possible. Groupishness has been ignored in large measure because of a deferral on the part of evolutionary psychologists to the theories of kin selection and reciprocal altruism (Cosmides & Tooby, 1992; Tooby & Cosmides, 1996) and their reduction of human cooperative behavior to the level of the dyad and family. Unfortunately, this ignores much about how humans behave as groups. As Boehm (1997) has argued, "with nothing more than kin selection and reciprocal altruism theories to work with, the selection basis of human degrees of altruism and cooperation is often difficult to explain" (p. S100). Such theories must be stretched to irrational limits in order to explain the types of collective behaviors that underlie not only rituals but many types of group behavior seen in human societies, things such as demonstrations, strikes, and riots, not to mention stereotyping and scapegoating (Hogg & Abrams, 1988; Hogg, 1992). There is a great need to develop a theory of *group-wide* cooperation (Boyd & Richerson, 1990),

and this is something that can only emerge from a group functionalist perspective of human behavior, for it is only group functionalism that allows us to conceptualize human cooperative behavior as groupish rather than merely nepotistic or reciprocalist (Boehm, 1997; Sober & Wilson, 1998).

The study of groupishness involves a cognitive and behavioral approach to two related aspects of human behavior: first, the tendency to form groups and to use groups as vehicles for individual survival; and second, a number of binarily-opposed emotive and motivational states that lead to positive behaviors toward members of the ingroup and negative behaviors toward individuals outside the group. Such oppositions take the form of empathy/antipathy, trust/mistrust, tolerance/blame, attraction/fear, attachment/distancing, identity/disidentity, and cooperativeness/destructiveness. At the social psychological level, this is manifested in the form of a universal propensity for what Donald Brown (1997) has called "coalitional thinking," a type of categorical thinking about "human kinds." Coalitional thinking nicely demonstrates the double-edged component of the group mind: group minds not only promote more efficient problem-solving strategies for group survival but also fuel competitive, ethnocentrist ideas about group uniqueness and superiority. Hirschfeld (1996) has reviewed the developmental psychological literature showing that the kind of categorical awareness that goes into coalitional thinking about human kinds (including racial thinking) is acquired very early on in psychological development, and Rabbie (1992) has summarized a large literature on so-called minimal-group studies that demonstrate the remarkable inclination of people to see intergroup relations in "we/they" terms, even when the groups in question are highly short-lived and completely fictitious. What these studies demonstrate is the human propensity to polarize, and to spontaneously associate positive evaluations with one's own group and negative evaluations with all others (Hogg & Abrams, 1988; Hogg, 1992).

In thinking about groupishness from an evolutionary standpoint, it is essential to explain its two major components: first, the tendency to form groups, and second, the suite of binarily-opposed emotional and motivational responses that reinforce it. The evolution of the capacity to form stable social groups, like any coalescence event in biology, comes about only through a reduction in competition between component units and a corresponding increase in cooperation between them. As several theorists have pointed out, human social behavior is characterized by a variety of mechanisms that are efficient at both reducing behavioral variation within groups and increasing such variation between groups (Boyd & Richerson, 1985, 1990, 1992; Knauft, 1991; Wilson & Sober, 1994; Frank, 1995; Boehm, 1996, 1997; Wilson & Dugatkin, 1997; Sober & Wilson, 1998). These include such factors as conformist traditions that homogenize behavior within groups (Boyd & Richerson, 1985, 1990), egalitarian ethics that level status differences between group members (Boehm, 1997), and social identity factors

that support group formation and bias individual behavior along the lines of group norms (Hogg & Abrams, 1988). Conformity, egalitarianism, and social identity are but three of a multitude of social processes that empower group selection as a force in human evolution. They do so by homogenizing groups internally thereby intensifying intergroup differences.

However what is typically missing from discussions of social control mechanisms in human populations is the more fundamental issue of group formation. I believe that social identity will turn out to be the most salient factor in understanding human coalescence and the emotive and motivational factors that reinforce it. Social identity is yet another critical psychological concept which has evaded the attention of evolutionary psychologists, this despite the fact that a century's worth of psychological experimentation and theorizing point to the central importance of social identity for human behavior. As early as the 1940's, the social psychologist Kurt Lewin pointed out that what defined a group was not merely similarity among individuals but instead a dynamic interdependence among them, and that the most important aspect of this relationship was interdependence of *fate* (Lewin, 1948). Many years later, Wilson and Sober (1994) reintroduced ideas along these lines in an evolutionary model of human behavior which had at its core the fitness consequences of shared fate for the evolution of group-level adaptations. However, what is more important than shared fate alone is *perceived* shared fate, and it is here where the concept of social identity (or what Lewin called "group belongingness") emerges as perhaps the most essential idea in the psychology of group behavior. The notion of social identity implies a collective acknowledgment of shared fate, and the recognition that coalescence and cooperation are necessary strategies for individual survival.

There is a large literature on the psychology of group behavior which demonstrates that social identity is perhaps the key factor influencing both intragroup and intergroup behavior, including the fundamental motivation to form groups (reviewed in Hogg & Abrams, 1988, and Hogg, 1992; discussed in Abrams & Hogg, 1999). Thus, the establishment of social identity might be the primary event that promotes both group formation[3] and the duality of ingroup-positive and outgroup-negative feelings that reinforce it. Shared fate is certainly an important ingredient in this formula, but group formation requires, in addition, an implicit awareness about human

[3] In passing, it is interesting to note that the notion of "identity" or "determination" is actively employed in the study of embryonic development in relation to the differentiation of cell types during tissue formation (Gilbert, 1997). This analogy can be applied to coalescence processes of any kind, and suggests that identity is a necessary precondition for coalescence. Cell sorting during tissue development follows the prior establishment of cell identity. Most likely, a similar process of identity establishment (self-identification in this case) is required for the formation of human groups.

categories and the importance of the group for individual need satisfaction and survival. Suffice it to add that social identity also has an enormous impact on the dynamics of social controls within groups, including such things as the conformist transmission described by Boyd and Richerson (1985).

To summarize this section, I have argued that multilevel selection allows us to understand the causal structure of biological phenomena in a way that than gene-centered or individual-centered explanations cannot. One component of multilevel selection is group selection. Group selection is probably a strong force in human evolution, and may be responsible for the complex trait I have called groupishness, with its coalition formation and suite of emotive and motivational traits that promote ingroup preferences and outgroup hostility. One offshoot of this syndrome is a type of group-wide cooperation and coordination that characterizes much human behavior in small-scale cultures, including the kind that makes up music and dance rituals. With this background, I can now move on to discuss a group selection model for music. Based on the above discussion, it should not be surprising to find out that music exploits our most groupish tendencies, both the positive and the negative.

3.2. Music as a Group-Level Adaptation

In this section, I will make a detailed argument that music is a group-level adaptation that evolved by group selection to increase the relative fitness of groups. I pointed out previously that sexual selection theory viewed music-making exclusively in terms of competition within groups, and completely ignored the cooperative nature and cooperative consequences of music. I concluded by saying that sexual selection functioned principally as an indirect selection mechanism secondary to a more direct form of selection. I believe that this latter mechanism is group selection, and that music's potential to be used as an aesthetic display and fitness indicator is secondary to its more general role in group function.

The following is a summary of my argument. The human capacity to make music is a group-level adaptation that evolved, in large part, by group selection. What this implies is the that the group, more so than the individual, is the appropriate level of analysis in thinking about the fitness consequences of music. Music's fitness advantages come about from its ability to promote group-wide cooperation, coordination, cohesion and catharsis, and this operates to increase both the absolute and relative fitness of groups. It functions to promote both group welfare and group warfare. The fitness benefits of music-making at the group level far outweigh the costs of individual participation in musical activities; music is, on balance, a low-cost system for the individual. There is little conflict between within-group and

between-group fitness consequences, and little motivational conflict between self-interest and musical participation. Music has a host of design features that strongly reflect its role in group function, the most prominent ones being pitch blending and isometric rhythms. Finally, music functions as a type of neural "reward" system, serving to emotively reinforce cooperative behavior during group ritual activities. Music evolved as ritual's reward system.

3.2.1. Music's Fitness Consequences Involve Increases in Both Absolute and Relative Group Fitness

What kind of framework can provide a reasonable basis for thinking about the fitness consequences of music from the group selection perspective? I will discuss music's role in reinforcing four generalized aspects of group function: group identity, cognition, coordination, and catharsis. Music will satisfy the criteria of being a group-level adaptation to the extent that it reinforces these general factors in the course activities critical to group survival. So long as we accept the argument that factors that promote either intragroup welfare or intergroup warfare contribute to the same final outcome in terms of relative group fitness, then there will be no need in making separate arguments for these two kinds of roles for music. Human groupishness is a two-sided psychological suite; ingroup cooperation and outgroup hostility are strongly linked to one another. To the extent that music can promote one, it can promote the other, and to the extent that it can promote either, it can increase the relative fitness of groups. It is not difficult to imagine the types of fitness-promoting effects that enhancers of group identity, cognition, coordination, and catharsis can have in terms of survival. We can choose to place the focus on ingroup-positive things like foraging efficiency, food sharing, cooperative group norms, altruism, social self-identification, and interpersonal bonding, or on outgroup-negative things like ethnocentrism, competitive edge, contests, warfare, genocide, and ethnic cleansing. Focusing on one should not obscure the fact that the other sits just around the corner. Music is a powerful force in human cultural behavior exactly because it is so effective at reinforcing both sides of the syndrome of human groupishness.

Therefore, I see no need to link the functions of music to specific behaviors, such as foraging or courtship. Music is a generalized emotive and semiotic enhancer which is powerful at influencing mass behavior. This effect often occurs in the context of group rituals, but in large-scale cultures music finds an astonishing variety of uses in the audiovisual media (i.e., film and television) and the sound environment (e.g., stores, restaurants, airports, doctors' offices). This power of music to act as an enhancer of anything with which it is associated leads to problems regarding the

morally-questionable uses of music, such as nationalist propaganda musics (quite widespread in the Communist world) and many forms of hate music. The power of music to foster group identity and collective resolve has been only too well recognized by dictators in the 20th century, and this has led to the frequent banning of ethnic-minority musics as a mechanism of social control. In thinking about music from a sociological point of view, we must keep this balance between use and control in mind at all times.

As with my discussion of the work of Arom and Khalfa above (Figure 1), I will describe how music's role at promoting group identity, cognition, coordination and catharsis manifests itself in form of *functional song types*. I believe that this is the only way that an evolutionary model of music will ever be able to have the sociomusicological sophistication necessary to bridge the gap between musical structure and social function, which is really the ultimate goal of the evolutionary approach to music.

1. *Group identity*. As described earlier, social identity is one of the most important determinants of human behavior. Given the intense groupishness of the human species, group identity markers are extremely important for self-identity. They are highly valued, personalized, and defended. Music is perhaps the most salient auditory feature of a culture, which is why it is universally acknowledged as being one of the most important cultural-identity markers, essential for signifying ethnicity, national identity, social class, and gender. As Stokes (1994) has written: "music is socially meaningful not entirely but largely because it provides means by which people recognise identities and places, and the boundaries which separate them" (p. 5). For example, from puberty Australian Aboriginal males start to the learn "lineage songs" about the totems and musical formulas that distinguish their culture from that of neighboring clans (Ellis, 1985). Political repression of such symbolic markers is a very effective means of suppressing group identity, such as occurred with the suppression of Aboriginal culture by the Australian government, or through the banning of all "national" musics by the nazis in the occupied territories during the Second World War, including disbandment of all the national orchestras in Poland and Czechoslovakia (Levi, 1994). In addition, people who are exiled from their homelands "sing the songs of home" (Nettl, 1983) as an important means of retaining their ethnic identity in a foreign and often hostile land, the occurrence of which has given rise to a rich repertoire of syncretic musical styles, such as all the African-American musical forms. Where historical migrations lead to a mixing of disparate cultures, music is perhaps the best means of reflecting the underlying mix of cultural identities, a

prime example being the Afro-Spanish phenomenon of Salsa music in Cuba (Negus, 1995). National composers, long dead, become national heroes, such as occurred in the case of Chopin in Poland (Mach, 1994), even though Chopin spent the better part of his active years as a composer living in France. While there, Chopin was able to retain his own sense of Polish identity by invoking typical Polish dance forms in his music, such as the mazurka and polonaise. At the regional level, this group-identification function occurs in the form of local musical dialects. As with linguistic dialects, these small but perceptible differences in musical performance style are ready indicators of what separates "our style" from "theirs," where "theirs" is invariably inferior to "ours." At the level of song types, this group-identity element is demonstrated in the form of national anthems, lineage songs, patriotic songs, songs of valor, songs of exile, songs of solidarity, and all songs that recount the characteristics or history of a culture, or the individual's identification with the community. It is also demonstrated at the local level in all the dialects that characterize group-specific musical variation in a region.

2. *Group cognition.* Human ritual activity can be thought of in a general sense as a form of group-level cognition. It is a type of collective thinking and decision making that reflects the operation of a group mind. It is here where we see music's essential role not only as a shared channel for communication but also as a major means of ritually marking key events in the life of the group. Music is an important mechanism for the transmission of group history and the planning for group action. This assumes a universal manifestation in the ritual chanting of sacred texts and prayers, the content of which invariably deals with matters of collective importance. It is probably no accident that ritual texts such as the Torah and Qur'an are never spoken but always chanted, as music is major means of conveying a feeling of sacredness or specialness in human activities (Dissanayake, 1988). Another aspect of this role is music's involvement in group problem solving, as presented in the form of such things as healing music, rain dances, sun dances, and shamanistic rites. But, perhaps most importantly, music's role at promoting group-level cognition is found in an abundant fashion in the historical songs (e.g., lineage songs, group epics), life-cycle songs (e.g., wedding songs, funeral musics), calendrical songs (holiday songs and seasonal songs), and narrative songs that fill the world's song repertoires. Music is one of the major means by which group ideas of all kinds are presented, maintained, and transmitted in a collective fashion for the purposes of recounting

history, preserving tradition, and planning for the future. We rarely use singing to convey information to individuals, but we very often use it to convey information to the group, especially in a ritual context. With regard to fitness consequences, music's effect on group cognition can be seen not only in promoting collective communication within the group but in defining and justifying group actions in relation to common purpose, historical tradition, and a shared sense of destiny.

3. *Group coordination.* Music is perhaps the ideal device for promoting coordination and cooperation at the group level, and the fitness consequences of such a function are far-reaching. This is mediated through both the rhythmic entrainment that occurs in metric music and through the pitch blending that occurs in group-wide vocal and instrumental performance, thereby promoting group participation, synchronization and "harmonization". Music's potential to promote coordinated action during work, a prominent feature of African cultures, was first highlighted in evolutionary models as early as 1896 by Karl Bücher. It is this coordinating function of music that allows us, perhaps more than any other human activity, to see human groups as organisms in a functional sense. But music's ability to coordinate people is not only used for action itself. Musical rituals are most often performed *in preparation* for group actions, such as hunting expeditions, foraging bouts, and battles, in which case symbolic re-enactment, in the form of theatre, story telling, dance, mime, and play, acts as an essential component of the ritual. Coordinated group activity in preparatory rituals serves an important goal in creating a sense of unity and shared involvement in the outcome of the group action at hand. The coordinating property of music is emphasized in such song types as work songs, rowing songs, and marching songs, but also in such preparatory forms as hunting songs, foraging songs, harvest songs, patriotic songs, and battle calls. Finally, we should not forget that even outside of ritual contexts, music's coordinating activity is found in a ubiquitous fashion in all the world's dance musics. There is no dance without music.

4. *Group catharsis.* Many of the things discussed above involve states of high emotion, as they are so closely associated with the issues of survival. In addition, interpersonal conflicts arise which threaten to destroy the stability of the group. It is telling to consider that music and dance are among the very few cultural mechanisms available for channeling group emotional expression, functioning as vehicles for generalized catharsis and conflict resolution, but most

importantly, as bonding mechanisms that generate spiritual solidarity and cooperation through shared, temporally-synchronized experience. These mechanisms are effective at both dissipating negative feelings and at crystallizing positive ones. And as mentioned above, they can be just as effective at exalting "us" as in dehumanizing "them." While language is certainly used to express emotion, music is the principal means by which emotion is expressed at the group level. In this category, we find play songs, protest songs, songs of oppression, lamentations, songs of mourning, celebrational songs, love songs, drinking songs, all songs expressing political sentiment, and most universally of all, all types of devotional religious songs that express love, fear and/or respect for a deity or ruler.

In sum, music's functions and advantages at the group level are so universal, dominant, and numerous that it is difficult to imagine a scenario for the origins of music that ignores them. Seeing music's fitness consequences in terms of the four broad categories of group identity, cognition, coordination, and catharsis allows us to see both the generality of music's effects at the level of function and the specificity of its effects for the level of the group. Music is a group-level adaptation that acts in a very general fashion in the life of the group. A group selection model of music does not necessitate that fitness-increases at the group level occur at great cost to the individual but only that a group can function as an organism, such that the shared fate of its components makes collective survival of the whole the best route for survival of its parts (Wilson & Sober, 1994). And in fact, music may be one of the few mechanisms that allows a group to act as an organism, not only in a metaphorical sense but in an actual sense.

3.2.2. Music Has Groupish Design Features at the Performance and Cognitive Levels

It was mentioned earlier that in music, as in all forms of animal communication, form reflects function, and that music has several design features that reflect a significant role in group function. I made this statement in the context of a critique of the sexual selection theory of music evolution. Yet to many people, this critique is counterintuitive because their own experience of music is based exclusively on the commercial music-culture of the West, with its sexy superstars and ever-present love songs. However, if the goal of this analysis is the think about music in evolutionary terms, then we must look to the musics of small-scale cultures, and most especially to hunter-gatherer societies. Only then can we decipher which features of commercial music are "ancestral" and which are "derived" (Brown, in preparation). Many Western notions of music are simply irrelevant to an

ancestral view of music (although the converse is not true). In fact, I think it is safe to say that the pop music culture that forms the basis of most Western people's image of music is the single most "derived" form of music (i.e., most diverged from the ancestral state) in the world today, hardly the basis for an evolutionary model of music.

It is therefore dangerous to use large cultures as a starting point in constructing models of the ancestral state of music, and this is because of some important sociomusicological correlations between musical structure and social structure and what they reveal to us about the cultural evolutionary processes that lead to the emergence of derived forms from the presumed ancestral state. As cultures expand in size and become stratified, many functional properties, including musical performance style, change in a dramatic way. At a fundamental level, a shift in social focus from the group to the individual occurs, as symbolized by the status of the ruling class of the culture. Musical strata evolve in a corresponding fashion through a progressive process whereby new strata are added onto pre-existing ones. The core stratum, ritual music, is present in some form in every culture. It is accompanied by a stratum of non-ritual music, something we can refer to as folk music. The next layer in the progression is the formation of classical music, which is the private music of the ruling class and aristocracy in a hierarchical society. This development is accompanied by a simultaneous expansion of folk music as an opposition not only to ritual music but to classical music as well. The last layer, which is added onto ritual, folk and classical musics, is commercial or popular music, which is a stratum found only in the technologically-advanced societies of the 20th century.

Between the extremes of hunter-gatherer cultures and large-scale industrialized societies, we see many intermediate levels of group size and social stratification. Such medium-sized cultures differ among themselves with respect to the emphasis they place on the group or the individual, as reflected in cooperative and competitive musical practices in their characteristic performance styles (Lomax, 1968). These two emphases can become segregated into different musical strata. For example, in any culture, ritual music will always retain the status as the most groupish and group-functional stratum of a large-scale culture, even when there are other strata, such as pop music, which explicitly glorify the individual. Likewise, these contrasting emphases can co-exist within the same musical forms through a combination of cooperative and competitive elements. By doing so, mixed forms are created, which contribute to the amazing diversity of musical forms and practices throughout the world. This notion of "mixed" musical forms is a reference to the opposition not only of cooperation and competition but of group selection and sexual selection. As music moves from the cooperative to the competitive, it also moves from the groupish to the sexual. It is no accident that Western pop music, the most derived form of

music in the world, is not merely soloist but sexual. And it is sexual not merely as a nonspecific fitness indicator and aesthetic display but as an unabashedly explicit message about conjugal love.

The major point here is that the opposition between group selection and sexual selection, with their respective emphases on group cooperation and individual competition, provides us with an important way of thinking about the ancestral state of music as well as the processes by which derived forms evolve. If we use large cultures as our starting point, with their many strata and mixed musical forms, we have great difficulties in determining which features of music reflect ancestral functions. However, when we examine small-scale cultures, *in which ritual music is the major stratum of the music culture*, we see that the structural properties, contexts, contents, and performance practices of music are overwhelmingly groupish and cooperative rather than individualist and competitive (see below). In such cultures, sexual display is secondary to the process of group assembly, not a primary motivation for musical expression.

The following list of ten points illustrates performance and cognitive features of music that strongly reflect the group nature of human music making. Briefly, music is a group-wide activity that encompasses people of all ages and both sexes. The principal contexts for music-making are activities of importance for collective survival; song texts and accompanying group behaviors reflect and reinforce this. The musical repertoires of small-scale cultures are organized into categories of discrete song types that reflect their associated social activities. Music-making both demands and produces cooperative teamwork on an unprecedented scale, serving to coordinate behavior both in preparation for group action and during it. Finally, the two defining features of music as a cognitive system, pitch blend and metric rhythms, are clear design features of music—completely absent in speech—that reflect music's origins as a group-selected trait. These points are now elaborated in detail.

1. *Group size.* As Lomax (1968) has detailed, musical performance style co-varies strikingly with group size (and thus with many structural parameters that covary with group size, such as subsistence style, power hierarchies, and sexual constraints). Perhaps the most important finding of his work is the demonstration that in small-scale cultures, performance style is overwhelmingly groupish, whereas only in larger-scale cultures, where there is a large degree of social stratification and hierarchy of authority, do we begin to see soloist styles emerging as major musical-performance arrangements. Lomax has shown that widespread use of solo singing is restricted to that style region which he calls

the "Old High Culture," comprised of the old civilizations of Asia (i.e., China, India, Southeast Asia, and the Arab world), where solo singing evolved as a device for the entertainment and glorification of the ruling class. This contrasts strongly with sexual selection scenarios suggesting that solo singing evolved from music's origin as a courtship device, as reflected in the oft-heard myth that "the first human song was a love song." It wasn't. Of this we can be reasonably certain. Soloist musical forms have arisen, for the most part, as reinforcers of self-promoting rulers, often at the expense of musicians who themselves retain a very low status in that society (for example, in northern India and all Islamic societies today).

2. *Functionality*. Functionality refers to the context-specific performance of functional song types, whereby particular songs are performed only in their appropriate contexts, and where the performers of these songs tend to be those people who engage in the activity being sanctified through song. It was described earlier with regard to the musical forms of the Aka Pygmies (Arom & Khalfa, 1998). Such is the case in cultures where music is a ritual preparation for action. Thus, among Central African Pygmies, women sing food-gathering songs, and do so in advance of or during food gathering expeditions but never at other times. Jews chant prayers before all meals (and sing such chants only then), reciting a prayer specific for the type of food being consumed. All people chant these prayers as all people eat. In shamanistic cultures, only the shaman (usually a man) is permitted to perform those ritual chants that induce a state of trance, thus expediting his psychic transport to other worlds. Again, such chanting is only allowed during appropriate ritual situations and not at other times. Thus, at the performance level, functionality maintains context-specific and/or role-specific performance arrangements, which often reflect a cultural division of labor.

3. *Both sexes*. The human singing arrangement is significantly different from that of all other animal species in that it frequently involves both sexes and all members of a social group. Group singing (called "chorusing") has been described in certain species of birds, but it shows none of the coordination of human singing. It tends to be nothing more than random simultaneity (Brown, Farabaugh, & Veltman, 1988; Catchpole & Slater, 1995). Whereas singing in humans often involves the whole group, the universal phenomenon of functionality implies that there are times when

only woman sing or only men sing, again, as small coordinated groups. This caveat implies that the role played by women in musical rituals may not be the same as, or even symmetric with, the role played by men. Such sex-specificity of functional song types is rather common among small-scale cultures. However, sex-specificity should not be equated with sexual display function (although it may certainly make good use of this), as functionality at the song level generally reflects gender differentiation at the task level, where music-making functions as a group coordination device in preparation for or during such tasks. The human singing arrangement, whether differentiated by sex or not, is unique among all singing animals, and clearly reflects the group structure of the human species.

4. *All ages.* The issue of age specificity in music is a complicated one. I don't believe that there is currently enough ethnographic data to provide any generalizations regarding this point. Clearly, group size and functionality considerations are critical here. The smaller the culture, the more groupish is the overall performance style (Lomax, 1968). In classless cultures like hunter-gatherer societies, there is simply *no distinction* between musicians and nonmusicians, and this means that there are no age restrictions when it comes to singing; everyone sings if they can. Children start to sing as soon as they are able to, as an important part of their socialization process. The oldest members of the group continue singing as long as they are physically able to do so. Louis Sarano recounts his experiences with the Babanzélé Pygmies: "Whenever those precocious four-year-old boys are drumming away on a battery of plastic jerrycans and tin bowls, you can be sure to find equally precocious four-year-old girls singing nearby. From what they attempt, it's clear they already know the ground rules for improvisation, they just don't have the technical ability yet to execute it properly. By the time they are teenagers they have the technical ability, and the genius, to sing music that sends shivers down the spine. At middle age, their music has the power to heal damaged souls. Certain older women may gain local renown as talented mime artists who dance out the stories in sung fables called *gano*; others become master storytellers, telling long stories alive with voices of a dozen characters and interspersed with songs" (Sarano, 1995, p. 18). Clearly, in such cultures, and in virtually all others, there are no general age restrictions as to who can sing. However, the real question is who *does* do the singing? At the level of the hunter-gatherer cultures, the answer seems to be that there are divisions of labor that characterize the work

group, as reflected in the functionality of song types (Arom & Khalfa, 1998), and that every member of the group who is capable of performing either the singing or the working does so, regardless of age. Cultures that deviate from this pattern, such as most large-scale cultures, are characterized by social stratification and sexual restraints on many levels, including the development of several differentiated musical strata. These things have a large effect on considerations of who sings and when. In such cultures, the distinction between musicians and nonmusicians becomes intensified to the point that musicians represent a minority specialization, often times restricted to family lineage (many societies) or outgroup status (e.g., the Gypsies of Central Europe and the Jews of the Islamic countries). In the largest cultures, where the commercialization of cultural objects abounds, there is a strong preference for young, attractive musicians in the stratum of commercial music. But this is a characteristic feature of commercial culture in general, and applies as much to film, television, dance, and fashion as to music. The overriding question here of whether there is an overall trend towards musicians being of peak reproductive age is, I believe, an open one, and unquestionably one which ethnomusicology should explore more closely.

5. *Group exclusivity.* To the extent that music is used as a group-identification marker, musical performance will be restricted to members of a particular social group. An obvious example of this is the fact that in Western societies, religious ceremonies tend to be restricted to practitioners of a given faith. Examples that might have more of a bearing on genealogical relatedness can be found in the Andean region of Peru, where one finds large populations of "mestizos," who are people of mixed native and Spanish origins. During many mestizo festivals, the nearby Quechuan community, comprised of indigenous rather than mestizo populations, is officially excluded from taking part in these festivals (Turino, 1997). Likewise, exclusion of the ex-slaves from white Protestant churches in post-Reconstruction America led to the formation of black churches of the Baptist, Methodist and Pentecostal varieties, each with their own unique musical traditions (Oliver, 1986). Group participation intensifies not only group cohesion but also group exclusivity, again, reflecting the double-edged nature of the group mind.

6. *Collectivist context.* This topic was covered in a general fashion above in the discussion of music as a group-level adaptation, in which music's roles for group identity, coordination, cognition,

and catharsis were outlined, as exemplified by the principal song types corresponding to each category. The context for musical performance in tribal cultures is as different as can be from the bird song arrangement, such that music tends to be restricted to occasions in which groups of people assemble for the purpose of performing some activity. That activity may be music alone, or it may be one of a large number of activities that deal with the business of group living and collective survival. Suffice it to add that courtship, reproduction, and the maintenance of group size are among the many functions important to collective survival.

7. *Collectivist contents.* Collectivist contents would seem to be implied from the notion of collectivist contexts. To the extent that music is associated with ritual contexts, it also tends to be associated with ritual contents, reinforcing the myths and normative behaviors of a culture. Thus the major emphases of ritual music are on honoring and obeying deities, respecting ancestors, performing socially positive behaviors, extolling virtues, recounting the origins of the group, transmitting group epics and myths, preparing for collective action, and so on (Merriam, 1964). Songs of conjugal love are either completely absent or are rare in small-scale cultures, thus arguing strongly against sexual selection scenarios of music origins (Sachs, 1948; Lomax, 1968; Arom & Khalfa, 1998). However, the comparative contents of the world's musical repertoires is very much an empirically analyzable body of data. One of the few people to look at song texts in a cross-cultural fashion was Alan Lomax as part of his Cantometrics project in the 1960's. Although he analyzed musical performance style in 233 cultures, his comparative analysis of folk-song texts was only a pilot study of 17 songs from six contrastive cultures. The purpose of this study was to generate a "concept profile" which would serve as a scale for analyzing song texts in general. In this very small sample, Lomax found that the four leading concept categories among the 17 songs were (in decreasing order of importance): time (words of being and condition, as well as words related to action upon the environment); the universe (the sky, the earth and the elements); communication (speech, music and dance); and social positive (all concepts related to good, right, beautiful, healthy, powerful and supportive at the social level, while minimizing any sort of conflict) (Lomax, 1968, p. 287). Obviously, not too much can be made of this small analysis, and no more comprehensive study has been undertaken since. However, it is telling to note that the concept-categories of "communication" and "social positive" were highest in the smallest cultures,

and lowest in the largest ones, once again arguing for important group-size effects on music at many levels. Much work is needed in this area.

8. *Pitch blend.* Space limitations prevent me from presenting a general analysis of musical phrase structure, but it is clear that the human musical system is by its very nature a system of pitch blending and patterning,[4] one that encourages group participation. Music is a two-dimensional system comprised of horizontal "sequence" and vertical "blend." Speech, by contrast, has only the horizontal dimension of sequence, and is used principally for dyadic communication rather than for group-wide expression. Speech proceeds obligatorily by an "alternation of parts," whereas music is highly effective at promoting "simultaneity of different parts" through its intrinsic capacity for pitch blending. Music's vertical dimension must be seen as a design feature promoting group performance and interpersonal "harmonization." Yet, not all forms of vertical patterning foster good blend. In fact there are at least nine different forms of polyphony in world musics (Zemp, 1996). However, in small-scale cultures, where groupish musical performance predominates, well-blended performance style is most common, and is highly valued for its symbolic feeling of unity. Good blend is best demonstrated in the polyphonic traditions of sub-Saharan Africa and the homophonic traditions of the Pacific Islands. In such cultures, individual showiness is discouraged, and good blend is culturally valued. Oddly enough, several forms of poor blend, such as Arabic heterophony, are probably no easier to achieve at the performance level than is good blend. Be that as it may, the major point is that the human musical system is one which is inherently designed for interpersonal simultaneity and group-wide participation, in a way that is inconceivable for conversation.
9. *Teamwork and coordination in performance.* Related to the issue of blend is the idea that musical performance requires a great deal of active teamwork. This is well documented in the very elaborate

[4] I have intentionally used the terms pitch blending and pitch patterning instead of harmony and polyphony in this chapter as the latter two terms have very specific meanings in musicology. Western-style harmonizing, called homophony, is found only in Oceania, Europe and the former colonies of the European powers. It is anything but the prototype of pitch blending in world musics. Be that as it may, thanks to the advent of commercial music and, more recently, to international pop music (so-called "World Music"), homophony has developed into a kind of infectious meme that seems poised at obliterating all other forms of pitch blending in the world. See Abraham and von Hornbostel (1905) for an almost amusing account of how homophony was imposed by a musicologist in a place it just never belonged.

choral singing and group dancing styles of the world. A wonderfully complex musical device that reflects this point is African "hocket," a system of total interdependence. In hocket, each member of the performance ensemble sings (or plays) one note or a small motif, such that coherent melodies can only be generated through the precise and ongoing alignment of these multiple parts. Such a technique is very common in Pygmy singing as well as in Haitian vodou music. The general technique of which hocket is a part is referred to as "interlock." Interlock is the general performance technique found in all sub-Saharan African musical styles (Arom, 1991), but is also used throughout the world in such disparate performance groups as Javanese *gamelan* orchestras and Andean panpipe ensembles. In such interlocked traditions, standing out above the crowd is officially discouraged. The ensemble should sound as one. Thus, musical performance in such traditions is about working together to create a common sound. This sound quickly becomes identifiable as "our" sound, which then becomes an important group-identity marker.

10. *Meter.* As Eric Clarke (1989) has pointed out, and as is apparent from watching the evening news, there is hardly a political rally in which people do not chant slogans a metric fashion. While speech never uses meter in a dyadic context, it uses it extensively in a collective context. Metric speech is the major means by which a group speaks in a collective fashion. Space limitations again prevent me from presenting a detailed thesis about the evolution of meter, however the simplest hypothesis is that the human capacity for metric time-keeping, which is a hallmark of human music, evolved as a group synchronization device during music- and dance-related rituals. This thesis places human time-keeping capacity firmly within a group-selectionist perspective, especially one that sees music as co-evolving with ritual. Yet not all music is metric. In fact, what a comparative view of world music suggests is that meter is used as a group coordination and synchronization device *when such coordination is needed or desired.* When it is not, musical forms will be in a freer, non-isometric rhythm. Therefore, soloist forms, especially those involving improvisation (like the *alap* of the Northern Indian raga, the *taksim* of the Ottoman Fasil suite, the *buka* of a Javanese gending, or a Qur'an or Torah cantillation) tend to be in a free rhythm, whereas ensemble pieces from these same cultures tend to be in an isometric or heterometric rhythm. Thus, musical meter functions as a coordination device in multi-part music or dance music, and seems to be

present only when such interpersonal entrainment is desired or needed. It is a device for coordinating vocalists with one another, instrumentalists with one another, instrumentalists with vocalists, and dancers with musicians. Again, when there is not a constraint to perform in a coordinated fashion, musicians throughout the world will often perform music in an unmeasured rhythm, especially, as has already been mentioned, where good improvisational skills are particularly valued in a culture. If we look at the predominant rhythm types of the different cultures of the world (Lomax, 1968), we see that freer rhythms are used in the soloist-oriented, improvisational forms of the large cultures, but that isometric or heterometric rhythms are the predominant rhythm types in the smaller, tribal cultures, where group-wide singing and dancing are the norm. Metric music and the human-specific capacity for rhythmic entrainment might be the strongest case for arguing that music evolved as a group cohesion and coordination device by group selection. Add to this the above argument that the capacity for pitch blending is inherent in the musical system and is well exploited in the musics of small-scale cultures, and we can say that music-making is the quintessential group coordination mechanism.

These last three points conform with evolutionary psychologists' preoccupation with "design features" for complex cognitive capacities (Tooby & Cosmides, 1992) by arguing that music is by its very nature a device which not only permits but promotes group participation and synchronization. This is reflected principally in music's capacity for pitch blending and rhythmic entrainment, which has led me to argue that the evolution of the neural modules mediating these functions occurred by group selection. However, I reiterate that music is a multifunctional object and that this short list has attempted to highlight the collectivist and groupish aspects of music-making, which are widespread.

There are many examples of musical forms or styles that are soloist, competitive, self-promoting, dyadic, poorly-blended, age-restricted, sex-restricted, asynchronous, monophonic, and so on. To the extent that sexual selection accounts of music-making highlight these features of performance style, they are complementary, not contrary, to the group selection account presented in this section. However, as I mentioned above, sexual selection scenarios tend to eliminate the specificity of music by reducing musical behavior to the level of nonspecific sexual display. What sexual selection models need to do is move beyond the display metaphor, and elucidate the extent to which sex and courtship have become specified in musical behavior and music itself, as reflected in the contexts and contents of music

making, in the features of global performance style, and in the formal and structural properties of music itself. In the end, if the evolutionary approach to music is to have any benefit at all for musicology it will be in directing future ethnomusicological research towards developing and testing hypotheses that can distinguish the effects of different selection mechanisms on musical behavior.

In closing this discussion of the group selection model of music, I want to make one last point. To the extent that music evolved by group selection, this must have been based on genetic variation more so than cultural variation, although the latter may explain many important features of music at the social level. The reason for this is that there is ample evidence demonstrating neural and cognitive specificity for music (Peretz & Morais, 1993; Marin & Perry, 1999), thereby suggesting that music is a genetically-mediated capacity shared by all human beings and not merely a culture-specific behavioral strategy or a culturally-selected meme. Music is a prime example not only of a universal human behavior but a modular function as well. Music is a self-contained grammatical system akin to language (Brown, 2000). Music is not just an art form but one of our fundamental ways of thinking (Gardner, 1983, 1993). The brains of musicians show several structural and functional differences from those of non-musicians (Sergent, 1993; Schlaug et al., 1995a, b; Zatorre et al., 1998). Musical consciousness exists in parallel to verbal consciousness (Brown, 1999). Universal properties of musics throughout the world can be described and classified (Brown, submitted a). In many ways, music is an ideal example of a cognitive adaptation of the type that evolutionary psychologists are seeking (Tooby & Cosmides, 1992; Miller, 2000), although it may be the first one described so far which is not explainable by individual selection mechanisms.

Music evolved in the context of collective rituals by group selection to make groups better survival machines, both against environmental pressures and against competing groups. Ultimately, this capacity for music came to characterize our species as a whole, and the ancestral state of music was born. As cultures diverged and expanded, musical behavior and music itself changed in significant ways. Different types of music-cultures evolved, devising new musical systems and novel uses for music. In this way, the elements that comprise the music-culture became complex memes, and the norms and roles that characterize musical behavior became important components of the survival strategies of each culture. However, to the extent that music is both a cultural universal and a modular neurocognitive function, we must entertain models based on genetic variation (in addition to those based on cultural variation), despite the constraints that such models impose.

4. MUSIC AS RITUAL'S REWARD SYSTEM

For many, music's evolutionary mystery is Darwin's paradox: that music requires such an investment of time and energy yet provides so little benefit for individual survival. But for me, the fundamental paradox of music is both deeper and more modern: that music has all the hallmark features of a complex and autonomous neurocognitive module, yet it has no autonomy at the cultural level (Brown, submitted b). Music is always about something else, about other activities and other meanings. But this point will certainly seem perplexing to people raised in Western culture, because the notion of a "concert" is such a prominent feature of our own music culture. However, it is essential to realize that concerts are a very recent human invention. In many cultures of the world, and most especially in tribal cultures, music is not performed for its own sake; there are no concerts and there is no passive listening to music in the privacy of one's bedroom. Music is inextricably associated with other activities, and most universally with group ritual activities. In addition, music is strongly associated with language, where it serves as a vehicle for the transmission of history, norms, and scriptures; music is an important device for making words sacred and memorable.

So here we have a true neural module, a cognitive adaptation, one of our seven intelligences, a self-contained grammatical system. Music has so much autonomy at the neurocognitive level yet so little at the social level. That, to me, is the evolutionary mystery of music. How can we resolve this paradox and move towards an evolutionary theory of music?

I believe that the only way around this is to say that music and ritual *co-evolved* in some very important sense during human evolution, and that in order to understand the role of music in ritual we must understand the role of ritual in human life. Ritual serves many important functions in the life of a group, including event marking, time marking, transmission of group history and identity, planning and decision making, preparation for action, social bonding, and conflict resolution. It is a means of sanctifying, marking, and making special (Dissanayake, 1988, 1992). Ritual represents the cooperative and groupish domain of culture. It is what happens when people put their group identity before their individual identity.

Merlin Donald (1991, pp. 175–176) has provided a fascinating and provocative account of the evolution of human cognition and culture. In discussing ritual, he writes: "Ritual, and its derivatives in theatre, differs from most other forms of mimetic representation in that it is a collective act in which individuals play different roles. A well-documented, widespread example from human Paleolithic cultures is the acting out of conquest, often without use of any words. A mimetic representation of the

enemy if accompanied by chanting, drumming, and communal mimetic dance. The essence of the mimetic act in this case is not in the action of a single individual but in the orchestration of several actors. Such representations are coordinated social efforts, dependent upon the actors', and the audience's, sharing a global cognitive model of society."

However music's role in ritual is not limited to wordless re-enactment plays but includes words, texts, and philosophies. Perhaps its most prominent role is in reinforcing the shared meanings and collective narratives of a culture, in other words, its myths. For Donald, "every aspect of life is permeated by myth (. . .) The myth is the prototypal, fundamental, integrative mind tool. It tries to integrate a variety of events in a temporal and causal framework. It is inherently a modeling device, whose *primary* level of representation is thematic. The pre-eminence of myth in early human society is testimony that humans were using language for a totally new kind of integrative thought" (pp. 214–215, emphasis in original). Music's role in myth occurs in the form of both the "chanting, drumming, and communal mimetic dance" alluded to above by Donald and in the direct association of music to a "totally new kind of integrative thought" through the singing of narrative texts, texts that describe the origins, history, personality, deities, norms, and virtues of a culture.

Donald offers little role for music in human cultural evolution beyond being an adjunct to wordless mimetic rituals. I would like to supplement Donald's "mimetic" account by describing a general role for music in ritual's development, thereby making this account co-evolutionary. An analogy to brain function would be useful. Many neural systems serve a purely informational function for the organism, encoding stimulus properties, controlling motor outputs, or mediating declarative memories. Other systems, called "modulatory" systems, are involved not so much in transmitting sensory and motor information as in conveying a sense of the *value* of an object or behavior for survival (Edelman, 1989). Such systems are reinforcement systems that attach rewards and punishments onto objects, thereby influencing the motivation to either move towards or withdraw from an object. If we extend this metaphor to the level of the social group, then we see that ritual is a type of informational system involved in encoding features of the physical and social environment, planning for action, transmitting history, and maintaining a sense of identity. In contrast, music is a type of *modulatory* system acting at the group level to convey the reinforcement value of these activities (or the information contained therein) for survival. Music evolved as ritual's reward system, a social neuromodulatory system. This view is supported not only by music's ubiquitous association to ritual activity in all human cultures but by the pleasurable and rewarding emotions universally associated with musical behavior and music perception. Music is not just an enhancer but a reward. It makes ritual

behavior motivationally salient for the individual. My basic hypothesis, therefore, is that *music and ritual co-evolved during human evolution, where ritual served as an informational system and music its reinforcement system.*

This view of music should make us reconsider the evolution of ritual from a biomusicological point of view. If there is a module for ritual behavior in the human brain, it is most likely the one for music. This is the only characterized module whose focus is on the collective side of survival, on what Lomax (1980) has called "the strategic models by means of which and in terms of which cultures endure." Was music the emotional justification for bringing people together, to have them feel a sense of unity, to have them sanctify that which is shared, to have them repel all that is foreign? In the end, music's salience is the salience of exactly those activities that Darwinists glorify. Music can be about foraging, but foraging is not about anything other than simple survival. We don't need ritual to remind us that we are hungry; we do need it to remind us that collective foraging is our best route to individual survival. Music simply convinces us that this has to be so.

5. CONCLUSION

Music has a wide range of functions. It is used for everything from assembling cattle to assembling soldiers, from playing games to initiating battles, from hunting animals to blessing food, from glorifying gods to condemning foreigners, from expressing romantic love to declaring political resentment, from exalting an individual's uniqueness to defining a group's identity, from uniting a city during a siege to commemorating its victims many years later, from celebrating life's pleasures to reinforcing one's duties, from cherishing fraternal ties to bemoaning sexual inadequacy, from transmitting creation myths to presaging group destiny, from remembering why one is alive to remembering those who have died. Yet, while music has this wonderful diversity of uses, the overriding theme seems to be centered at the level of the group, especially in terms of group identity, cognition, coordination, and catharsis. The notion that music-making affords opportunities for sexual display takes advantage of the very fact that music is a group behavior, one which brings all members of the courtship game into close contact. But courtship is simply one more domain in which music has found an important role in human cultures. There is an abundant number of contexts in which courtship and sex serve no role at all in musical rituals, and in which any display role afforded by music-making is an indirect consequence of the group activity at hand. So courtship should be viewed as one important context and function for music-making, not its *raison d'être.*

A cross-cultural view of musical performance style strongly supports the role of music in group function. Music has adaptive design features that reflect this role, such as its use of pitch blending and isometric rhythms. I have proposed a group selection model for the evolution of human musical capacity, one which openly acknowledges the highly double-edged character of human nature: music is just as useful for bringing out our killer instincts as it is for inspiring our most high-minded and ecstatic sentiments.

In discussing music's adaptive function, two evolutionary paradoxes came up. First there was Darwin's paradox about the high cost but minimal survival benefit of music for the individual. Then there was my own evolutionary psychological paradox which says that while music has all the requisite features of an autonomous neurocognitive module, it acts in a completely non-autonomous manner at the social level. My solution to both paradoxes led to a common view of music as a group-cooperative device that evolved with the emergence of group rituals during human evolution. Music's role in ritual is both general and specific. It is general in the sense that music functions as a generalized reinforcer of all types of ritual activities and symbols. However, its role is specific in the sense that music evolved as a reward system rather than a punishment system at the group level. It makes individual investment in group rituals a cultural imperative. Music is a group-level modulatory system, ritual's reward system.

I have argued that music is a group-level adaptation because of its ability to promote collective survival. But as we all know, much has been done throughout history in the name of collective survival. Dmitri Shostakovich, whose Seventh Symphony was mentioned at the opening of this chapter, was vehemently attacked by the Stalinist regime during the 1930's and 40's exactly because his modernist music was considered to be a threat to collective survival. He became the most renowned victim of artistic repression in Stalinist Russia. He squelched his creative tendencies as the most brilliant composer of his generation to become something of the obedient composer-of-state of the Soviets, and even then did not evade devastating public censure on two occasions. Much the same kind of manipulation of composers and musicians occurred, but on a much more insidious scale, in nazi Germany, where the "degenerate music" of the atonalists, Jews and Blacks was outright banned, and where music was used as a propaganda device in a manner that still inspires modern-day manipulators of music. Music is a prostitute. It is used for whatever purposes people have in mind. It can promote hate as much as tolerance, division as much as unity, idleness as much as action. All these things emerge from a view of music acting not as a display behavior in a fixed context but as a flexible semiotic enhancer and emotive manipulator that operates within complex and often irrational systems of cultural meaning. Such things that can only be appreciated from a group-functionalist perspective. In the end, multilevel

selection provides a much broader and richer view of music than individual selection.

Whether music evolved to woo the hearts of women or to promote the survival of social groups, there is no question that it has been one of the most important forces shaping cultural behavior during human evolution and in all contemporary societies. The time has come for those interested in the evolution of human culture to realize that music offers a veritable treasure trove of insight into how we act, how we think, and how we feel . . . both individually and collectively.

ACKNOWLEDGMENTS

I thank Nick Thompson for invaluable discussions about group selection and altruism during the writing of this paper, for his extensive editorial comments, and for the opportunity to publish this chapter in the current volume. I thank Gerhard Schlosser (University of Bremen) and David Sloan Wilson (Binghamton University) for critical commentary on the manuscript, and well as for discussion of important issues during the writing of the paper.

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Chapter 10

BIOLOGY, CULTURE, & RELIGION

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1. INTRODUCTION

Scientists often point out that most of the beliefs purveyed by religious systems are incompatible with modern scientific knowledge. That discussion has been going on since the Enlightenment, and especially since the publication of "The Origin of Species". As a recent example, Dawkins (1993) has likened religion to a virus, and referred to religious belief as involving an "infected mind". The implication of his writing is that humans would do fine if they trusted to scientists, who Dawkins defines elsewhere as "the specialists in discovering what is true about the world and the universe", and could reject "bad or silly traditional information". Of course Professor Dawkins is right in saying that the basic beliefs, if taken literally, are simply unacceptable to most twentieth century minds. Stories of the Virgin birth, of Resurrection and Ascension, require more than a pinch of salt. And school teachers must no longer be expected to teach about specific gravity in one lesson and talk about Jesus walking on water in the next. Of course, science can do a better job in helping us to understand our origins than can Genesis or any comparable myth. Of course, science is better fitted to help us understand the relation between cause and consequence in everyday life. But to reject all religion because religious beliefs are incompatible with modern scientific knowledge is unsatisfactory for at least three reasons.

Perspectives in Ethology, Volume 13: Evolution, Culture, and Behavior
edited by Tonneau and Thompson, Kluwer Academic/Plenum Publishers, New York, 2000

First, belief in dogma is by no means all there is to religion. Most, but by no means all, Christians give it primacy—"Believe, and ye shall be saved". But belief is not central for many religions, such as Hinduism and Buddhism. Every religious system involves at least six interdependent elements: Structural beliefs, such as the Christian Trinity; Narratives, such as the Gospels; Ritual; a Code of Conduct; Religious experience; and a Social element. The relative importance of these elements differs between religions, and some religions may lack, or appear to lack, one or more of them. Since the elements are interdependent, I refer to the collectivity as a religious system.

Second, a purely destructive approach is unsatisfactory because it is unscientific. Religious systems have been ubiquitous throughout human history. In spite of their clearly counter-intuitive nature, religious beliefs of some sort have been held by the vast majority of humans. Surveys of scientists in the USA in 1916 and 1996 showed that the proportion who believed in a personal god who heard prayers and could grant immortality remained steady at about 40% (Larson & Witham, 1997). So clearly there is a scientific problem here. Why have religious systems occupied a position in human life almost as important as procuring food or achieving reproduction? There are only two alternatives. Either religious systems concern some transcendental truth, or there must be an explanation which rests ultimately (though not necessarily immediately or obviously) in human nature, and thus is likely to be Darwinian. And that must be an explanation that not only encompasses more than the beliefs, but also is concerned with both the positive and negative consequences of religious observance. Rather than pitting science against religion as alternatives, we should use the former to understand the latter. This is the principal topic of this paper.

Darwinian explanations of religious systems are potentially of two sorts. One aims to show that adherence to a religious system is itself adaptive for individuals: previous attempts in that direction (e.g., Reynolds & Tanner, 1983) have not been outstandingly successful, principally because, I believe, they involved too complex a level of analysis. The other focusses on basic human propensities that contribute to the religious system, not on religious observance as a whole. This requires a slight digression.

Just as we all have certain anatomical characteristics, such as the patterns of ridges and furrows on our fingers, though these patterns differ slightly between individuals, so we all have certain psychological and behavioural characteristics, though the extent to which these are manifest also differs between individuals. Most importantly in the present context, and easily overlooked as a commonplace, we all have certain needs or goals, and the ability to use variable means to attain them. These needs or goals include not only the more obvious ones of food, water, and sex, but also such more intangible issues as the need to make sense of the world by

attributing causes to events, the achievement of status, and feelings of self-efficacy and security. In this paper I suggest that religious systems are seen here as resulting from interactions between such basic propensities.

To understand fully almost any aspect of human behaviour, it is necessary to recognise the mutual influences between a number of levels of complexity—psychological processes, individual behaviour, interactions, relationships, groups and societies. Each of these levels has properties not necessarily relevant to other levels, each affects and is affected by the others, and each affects and is affected by the "socio-cultural structure" of beliefs, customs, norms, values, institutions, etc., accepted by those involved (Hinde, 1987, 1997). This socio-cultural system includes the religious system. But that does not imply that either the socio-cultural system as a whole or the religious system is static and unchanging. Rather they are to be seen as dynamic, created, maintained or degraded by two-way influences, synchronic and diachronic, with the levels of social complexity. These mutual influences within and between levels produce psychological characteristics and behaviour that may be adaptive or maladaptive for individuals.

It is not essential to the argument that all the propensities to which I shall refer are or have been adaptive in the biological sense—that is that they have fostered the survival or reproduction of individuals. As a matter of fact I do believe them all to be products of natural selection, but some could be by-products, spandrels as they have come to be called (Gould & Lewontin, 1979), and in any case as yet we know little about their ontogeny. That issue is not central to the present argument: the emphasis is on their ubiquity. The suggestion is that, in religious observance, such basic human characteristics are deployed in contexts different from those in which selection originally took place. The question of how far religious systems can be understood in terms of basic human psychological characteristics suggests a third reason why we should hesitate before we take a purely destructive approach. Religions (and I do not mean only Christianity)[1] have upheld values of love and respect for others which have been fundamental for the smooth running of societies. They have helped individuals to face injustice, suffering, pain, and death. Concentration camp inmates, prisoners, and citizens under stress with strong religious or religio-political beliefs have done better than those without them. Of course religions have also been used to perpetuate inequalities, to justify torture, and to incite hatred and participation in religious wars. But if some people have found religion helpful for

[1] In this paper, for reasons of space and my own familiarity, it is primarily Christianity with which I shall be concerned, but, as discussed at greater length elsewhere (Hinde, 1999), the principles apply much more widely. A useful survey of other world religions is given by Smith (1991). For a review of the methods used to study religiosity, the reader is referred to Brown (1987). For a survey of the sociology of religion, see Bruce (1996). The psychology of religion has been discussed recently by Hood et al. (1996), and Wulff (1997).

some of the time, we must surely endeavour to find out why and to specify the circumstances and religious orientations that lead to their desirable and their undesirable consequences. This leads to questions concerning exactly what is desirable and undesirable, whether we should retain religious practices and beliefs or not, and, if not, with what we should replace them. These are issues that can be only hinted at here.

One concept used in what follows is that of the "self". The devout Christian may speak of "giving himself to God", but what is this "self" that he is giving? The "self" is not a thing, but a concept we use to understand certain aspects of our behaviour and that of others. Thus we change our behaviour to suit the context that we are in, but we still feel that we are the same person, the same "self". From time to time one may feel angry with "oneself", and reflect on what one's "self" has been doing. One may plan what one's "self" will do to-morrow. The religious system becomes part of the religious person's "self". We assume that other people think in terms of their "selves" too. We need not worry what it means to say that someone "has" a "self", or ask where the "self" is—it is merely a concept useful for explaining the continuity in our lives and integrating the world in which we live. For present purposes we can regard the "self" as summarising the various ways in which individuals see themselves (Hinde, 1997). Its relevance in the present context is that the "self", the idea one has of one's own nature, is a powerful determinant of one's behaviour and personality. Furthermore, we protect the integrity of the "self" in a variety of ways, including the use of defence mechanisms (Backman, 1988).

2. THE ELEMENTS OF RELIGIOUS SYSTEMS

2.1. Structural Beliefs

To start with the structural beliefs, most religions involve a belief in some sort of transcendental entity or entities which are related to, but in some sense distinct from, the world in which we live, and are usually independent of time. Sometimes the entity is immaterial and impersonal. Some physicists are struck by the elegance of the Laws of Nature and, forgetting that beauty lies in the eye of the beholder, they see them as embodying an absolute goodness, lying out there in the world. Some modern intellectualist theologians argue that God is the essence of supreme and unimagineable goodness. Some eastern religions refer to an all-pervading force or essence, though this is at times and to varying degrees anthropomorphised. To the Hebrews, Jahweh had no tangible characteristics. To Gandhi God was Truth, Love, Ethics and Morality. But God or gods are more usually

seen as organismic, and most usually as anthropomorphic, with both human and superhuman characteristics. This is true of all the main world religions (e.g., Carrithers, 1983; Zaehner, 1962) and, with Christianity and the eastern religions, especially the case with the less literate members of society. And it is with the lay-person's view that we must be concerned if we are to understand the persistence of religious systems.

Belief, of course, covers a spectrum of meanings (e.g., Brown, 1987). For the fundamentalist, its meaning is absolute. The dogma of the creed is accepted as divinely given and not to be questioned. A religious believer may simply accept the structural beliefs and the narratives, and is just not concerned about their internal contradictions or incompatibility with modern knowledge. He or she may take, consciously or unconsciously, a "step of faith" such that the contradictions do not matter. Religious truths are seen as different in kind from the scientific truths of the world we live in—an attitude regarded as a cop-out by many non-believers. For others, "belief" is not the same as "certainty", but merely means "I will act as if it were true". Belief may be basically emotional, but intellectually supported. And some, including the authorities of the Church of England, have argued that religious statements, if not literally true, nevertheless have value as "spiritual truths".

2.2. Why Believe?

In any case, we may ask why individuals hold religious beliefs. Do they satisfy basic human needs? Many have seen religion as a source of comfort: Marx described it as "the sign of an oppressed nature", and Weber argued that the need for salvation is an expression of distress, so that religions involving redemption appeal strongly to the underprivileged. Others have seen it as a means of coming to terms with death, and yet others have argued that belief systems interpret the world and give meaning to life.

Perhaps the most encompassing answer involves the suggestion that religious belief provides for a number of basic propensities, common to all humans. Of these the most important would seem to be the propensity to attribute events to causes and so avoid the feeling that our lives are subject to random forces, the need to feel that we have some control over our lives, the fear of death, and the need for personal relationships and support.

Considering first attribution, we all try to understand what is going on around us by seeking causes for what happens (e.g., Planalp & Rivers, 1996). In everyday life we use principles with which we are already familiar—if we see a tree blown over, we attribute it to an exceptionally strong wind or to rot in the trunk. We ascribe other people's behaviour to internal states ("He is running away because he is frightened") and may make use of a

theory of mind (He is running away because he knows that his rival is out to get him"). And if the event is inexplicable, we invent an agent to account for it ("Luck was on her side"). Thus an entity that could be seen as causing otherwise inexplicable natural events, such as rainbows or the eruption of volcanoes or the origin of the world, would satisfy a basic need in providing the illusion that one understood the world. Many gods would seem to play just that role.

Of course, we need to understand adverse events as well as neutral or beneficial ones—hence the postulation of malevolent beings, witches, and evil spirits. In World War II Royal Air Force aircrews were prone to ascribe anything that went wrong with their aircraft (and even their own errors) to "gremlins"—mischievous sprites who took a delight in causing problems. The interesting point is that although gremlins not only filled an explanatory gap but also provided a route for a half-joke about an issue that could spell disaster and a means for deflecting blame from aircrew or maintenance staff, they were not really believed in: in that respect they were not so different from the beliefs of many religious adherents.

But we also try to control the events that influence our lives, and our well-being depends on our belief that we are able to do so. The importance of a feeling of "self-efficacy", that is, of belief in one's ability to organise and execute the actions necessary to reach one's goals, has recently been documented by Bandura (1997). Entities who could help one to achieve one's goals have enormous appeal. A god who would intervene, who would help you if you asked nicely, would be even more attractive than one who merely caused natural events. This is in harmony with the fact that powerlessness, illness or adversity tend to enhance religious belief.

Not all deities are thought of as intervening in the world, but another source for belief in them lies in the desire for life after death, itself perhaps related to the need for a feeling of self-efficacy. Non-existence is almost impossible to imagine, as it is impossible to imagine oneself unable to imagine. Life after death implies belief in spirits of some sort—spirits which must be somewhere and so may continue to inhabit our world or live in some sort of spiritual abode. Christians have Heaven and Hell and perhaps Purgatory, and other religions an extraordinary variety of abodes for the deceased.

Furthermore, belief may have a strong emotional component, the deity providing the illusion of a personal relationship. Believers may feel that they have a relationship with the deity which has many of the characteristics of a human relationship and involves feelings of trust and reliance, a relationship with someone who will always be there and with whom they can talk over the day's events, and on whom they can rely in times of trouble. A believer may even see herself as a "bride of Christ". As a result

of the work of John Bowlby (1969/82), psychologists now recognise that the provision of a secure base by a caring adult plays an important part in personality development, and that a feeling of security is of critical importance throughout adult life: some get that sense of security from religious participation.

It is thus apparent that, while generalisations about why people hold religious beliefs are liable to be simplistic, such beliefs can satisfy needs which are pan-cultural characteristics of human beings. At least some of the issues can perhaps be integrated by saying that religious involvement can provide a coherent view of the world. But surely, one may say, nowadays science provides explanations for the events we wish to account for, and tells us that many of the events recorded in the scriptures are implausible? Indeed so. But there are three problems with a purely objective view. One is that most people have difficulty in seeing how science could account for events that seem to occur by chance, and it is just such apparently haphazard events that puzzle people most. Why did the tornado strike here and not there? Why did this man and not that get knocked over by the bus?

Second, belief is not solely an intellectual matter. Belief may provide satisfactions, perhaps fulfilling relationship needs, that the individual is denied in real life. It may provide for emotional needs: before an operation, many would find it more comforting to be told "God will look after you" than "You stand a one-in-twenty chance of coming through".

And, third, the acceptance of mortality runs counter to biological propensities conducive to survival, and involves acknowledging that we have only limited control over our lives, thereby diminishing our sense of self-efficacy. Belief in an after-life can be comforting.

Furthermore, belief is seldom a matter of considered decision. Rather, religious beliefs and practices are usually soaked up in the course of socialisation: they are acquired in much the same way as children learn how to behave in social situations. The acquisition of ways of behaving from other individuals is certainly a universal human characteristic, and there is evidence that it has been selected for in the course of evolution (Boyd & Richerson, 1991). Thus the acquisition of religious beliefs involves processes that seem to be identical with those normally operating in socialisation.

Nor must it be forgotten that belief is not just an individual matter. Individuals often gain from the sense of community provided by a religious system, and a gain to the community from the loyalty of individuals is thus engendered. This social element is enhanced in another way. People tend to be attracted to others who share their attitudes, and experimental evidence indicates that such attraction is especially strong if the shared attitudes involve otherwise unverifiable beliefs, because thereby consensual validation is obtained (Byrne, Nelson, & Reeves, 1966).

2.3. The Nature of Deities

Now let us consider the nature of the religious entities that are postulated. Developmental psychologists have shown that children distinguish animate from inanimate objects primarily (though not solely) on the basis of their capacity for self-propelled locomotion. Animate beings can initiate action, inanimate objects cannot (e.g., review Karmiloff-Smith, 1995). It is thus natural that otherwise inexplicable events should be attributed to animate beings. Indeed, as Lewis (1995) has suggested, the very notion of cause may stem from the subjective experience of making something happen. Furthermore, the evidence that the evolution of human cognitive abilities was primarily due to selection for competence in dealing with other individuals is becoming increasingly compelling (Humphrey, 1976), so it may also be expected that animate causes should be seen as human. Indeed it seems to be a general human characteristic to tend to make anthropomorphic attributions. This tendency may be augmented by the consequences of dreaming: all humans dream, and dreams concern beings with human-like properties. The Australian aborigines saw the origin of the world in a dream-time, and dreams play an important part in many religious systems. Traditional Chinese tales indicate that dreams were perceived as real (Dudbridge, 1995).

But deities, whether or not human-like, also have special properties. They combine everyday characteristics, usually of human beings, with counter-intuitive and improbable properties, such as abilities to rise from the dead, walk on water, heal the sick, and so on. Gods may conform to many of the properties of human beings: they can be loving, forgiving, sorrowful, or angry. But at the same time they may be omniscient, omnipotent, and ageless. Boyer (1994) has suggested that religious entities must involve a balance between counter-intuitive and therefore attention-getting properties, and other properties that are in harmony with everyday experience. Such a balance is necessary because without the former the gods would not be interesting or memorable, while if there were no everyday properties and all characteristics were outside our experience, we should not be able to relate to them or remember them. The everyday characteristics also permit further inferences—if a god has desires, one can make inferences about how he will act. To take an example from folk-lore, one remembers ghosts because they are transparent and can pass through walls, but that tells us nothing more about what they are like. But if they wail we can assume that, like humans, they experience unhappiness.

Such a combination of improbable and everyday properties may be important not only for deities. In Britain, and also in many other countries throughout the world, the death of Princess Diana was followed by remarkable demonstrations of public loss. Hundreds of thousands gathered in London to see her funeral procession; millions watched it on television;

people queued for many hours to sign the books of condolence; the bunches of flowers left at places associated with her were uncountable. Such a public demonstration must surely have been related to the way in which her public image included an extraordinary combination of improbable and everyday characteristics: she was regal, rich, beautiful, remote, and yet at the same time human, suffering, and intensely humane, validating the values to which many aspire. In harmony with this suggestion, in the Christmas after her death a figure of Princess Diana was included with the Virgin Mary in thousands of Neapolitan Christmas cribs.

Gods are often seen to act in diverse ways. In some pantheons, the several gods are assigned different characteristics—some are benevolent, some are cruel; some male, some female. In other cases, gods are ambiguous, having more than one personality, just as we present a different self in different social situations. The Hindu Shíva is seen as the reconciliation of opposites—creator and destroyer, good and evil, male and female. His consort is both part of himself and separate from himself, and is likewise seen as both the mild Parvati and the blood-swilling Kali (Zaehner, 1962).

Christians, in reconciling their God with monotheistic Judaism, met this problem in a different way—God is held to exist in three Persons and one Substance, Father, Son, and Holy Spirit. The Father is seen as ungenerated and responsible for the Creation; the Son combines human attributes with miraculous powers; and the Holy Spirit is seen as the intermittently active but impersonal power of God, acting initially in the New Testament through Jesus, but lacking human properties. Thus the problem of the Creation and the combination of intuitive and counter-intuitive properties are solved by the notion of three "Persons" in One.

Of special interest in this context is the status of the mother of Christ. Mentioned only somewhat briefly in the New Testament, she has become a central figure for many Christians. Her image has taken on many different flavours—in part through the manipulations of secular or religious leaders and in part through popular demand—so that her virginity, her regal attributes, her maternity, her humility, her role as an intercessor and other characteristics have been emphasized to different extents at different times (Warner, 1976). At the time of writing the Pope is believed to be considering a proposal that she be seen as "Co-Redeemer" with Christ.

3. NARRATIVES

The second element in a religious system consists of the narratives. For Christians, these involve primarily the Gospels and also the other books of the New Testament, and for some the lives of the Saints. The narratives

are usually based around issues of individual or social concern—the relations between ruler and ruled, the mysteries of birth and death, sex, wealth and poverty, and so on. Everyday matters appropriate to the society in question are interwoven with the supernatural. The setting is also culturally appropriate: thus the Christian God is portrayed as sitting on a throne in a situation resembling a mediaeval court, especially in post-Biblical literature and art. The properties of that court are explained in terms of the secular, Middle Eastern preoccupations of that time. Thus descriptions of Heaven in the Book of Revelations resound with references to gold, precious stones, and light. In China jade took the place of gold in the heavenly realms (Rawson, 1995). In both cases the properties of heaven are symbolised by the same sort of material objects that indicate value in ordinary life—and there is evidence that in pre-industrial society the possession of such objects was associated with reproductive success (Betzig, Borgerhoff, Mulder, & Turke, 1987).

The narratives are closely related to the structural beliefs, which they exemplify and extend. The use of the narrative form is exactly what one might expect from our use of narrative in everyday life. We see the past as a series of loosely connected episodes, and we see the future unfolding as a narrative. Narratives help us to make sense of the world. We make extensive use of narrative in teaching our children (Bruner, 1990).

The suggestion, then, is that religious narratives involve the use of a ubiquitous human tool to make a more or less improbable message the more acceptable because it is presented in a recognisable setting.

4. RITUAL

We may turn now to the category of religious ritual. This, like religion itself, is far from easy to define. It usually involves a series of actions which are repeated from time to time in a fairly rigid sequence and are seen as distinct from everyday actions. Ritual behaviour is said to differ from everyday behaviour in that it "stands for" something over and above the actions performed, though the exact nature of that something is hard to pin down, and may be idiosyncratic. Most rituals are acquired by children from exemplars and are seen as "what one does" on particular occasions: only gradually do children become aware of the adult "meanings" of the acts involved.

Ritual behaviour is not, of course, peculiar to religious systems. The procedures and actions that mark the family Christmas dinner, or even the family evening meal, have characteristics in common with religious rituals. Indeed religious and secular rituals are often interwoven, as in Remembrance gatherings for those killed in war.

4.1. Why Do People Take Part in Rituals?

Whilst those present on a ritual occasion may be there for a great variety of reasons, it is convenient to distinguish between the religious specialists, the central figures (if any), and other participants or spectators. Two types of specialists can be distinguished. The first is characteristically initiated into the role by a special ceremony (such as ordination) or, in societies that make less distinction between religious and secular affairs, holds a certain rank (e.g., chief). The others are recognised as religious specialists by virtue of their charisma. In some cultures both types co-exist. However each may include features relevant to the other: for instance specialists of the former type may try to reinforce their position by assuming a certain charisma. In our society we tend to see priests as having certain personal qualities, even though these were not necessary qualifications for their role. Boyer (1994, 1995) has suggested that this is a carry-over from the way in which we use categories in the natural world. We tend to see living things as not only identifiable by certain typical features but also as having an underlying essence which is present in all exemplars of the category. Thus a tiger is still a tiger and is still seen as having "tigerishness" even if it loses its teeth and its stripes are shaved off. The powers that religious specialists are seen as having, and the standards we expect them to show, are partly consequences of qualities that they are expected to have and that are ascribed to them by others.

Participation in the rituals by the religious specialists hardly needs explanation—it is one of the duties associated with their role. Most of them must believe in the authenticity of the performance. A few may be involved merely out of habit, or in hope of preferment. There may be an unconscious desire to maintain the belief system, perhaps because their own position depends on it.

Central figures among the other participants may be the foci of a *rite de passage*, marking transformation to a new life stage or entry into a new relationship. Their participation, like that of the priests, may be performative (Austin, 1975): the words "With this ring I thee wed" are the act. In initiation ceremonies the central figures may participate in or endure the ceremonies in expectation of the status to be conferred on them.

For other participants, each may have a different reason for being present. They may attend to watch the couple being married or the adolescent initiated, but a host of other motivations, conscious or unconscious, may lie beneath this. They may be recollecting or imagining the day on which they were or will be the central figures in such a ceremony. They may be seeking a sense of community, or validating their own role in the community. Or the ritual may be sought as simply expressive, satisfying a desire for dramatic participation, or bringing desirable cathartic consequences.

Where the ritual is disturbing or frightening, they may be seeking arousal. But any generalisation is dangerous, for each participant may read a different meaning into the ceremony (Humphrey & Laidlaw, 1994).

4.2. The Consequences of Ritual

But what are the consequences of religious rituals? Here it is important to distinguish between the supposed purpose of the ritual, the experiences of those involved, and other consequences as perceived by an outside observer. The supposed purpose of the ritual—to marry a couple, to worship the deity, to heal a sick person—will be closely related to the belief system. Whether or not the ritual is seen to have achieved its supposed purpose depends in part on whether it is seen to have been performed correctly, and whether it is seen to have been performed properly depends in part on whether it is seen to have achieved the desired consequences. Thus a ritual performed to cure sickness, but followed by no improvement to the patient, may be assumed not to have been performed properly, either because the proper sequence of acts was not followed, or because the religious specialist conducting the ritual was not properly qualified, or because necessary (but perhaps as yet undefined) background conditions were not met (Boyer, 1994).

In most Christian services, the most important consequences are those on the participants or congregation. These will depend, of course, on their motivation for attending. But ritual involvement may have profound effects on the self-systems of believers. In the case of *rites de passage*, the ritual creates or marks a new social identity and a new self-image and self-system for the central figures. They see themselves, and others see them, as "now married" or "now full members of the church". Initiation ceremonies that involve suffering may result in a diminution in personal identity and enhance identification with a new category of persons—consequences which may be important both for society and for the individual. The principal participants may be better able to see themselves in their new roles after the ceremony. So also will the congregation, for they must change their relationships with the principal participants, requiring a change in their self-systems. This is especially the case with a funeral, where the ceremony indicates the end of, or at least a change in, the relationship with the deceased, or that the deceased has acquired the status of an ancestor. The ceremony may also have the consequence of increasing social cohesion: in a wedding ceremony the two families are drawn together, and in an ordinary service the bonds of a community are reaffirmed.

Finally, an outside observer may identify further consequences of a ritual. Thus Turner (1967) suggested that a particular Ndembu ritual per-

formed for a woman suffering from leprosy also reduced the hostility of the villagers to the woman, many of whom had seen her as a witch, by making her an object of sympathy; closed a breach between different factions in the village; gave prestige to the host village; re-established relationships with other villages; and exemplified Ndembu beliefs and values. Of course, while these may have been consequences of the ritual, there is no evidence that they were intended or that they were important in the maintenance of the ritual.

4.3. Prayer and Sacrifice

Prayer can be seen as a form of ritual affirmation of belief in a supernatural being. But such affirmation may in itself address more mundane needs. As noted above, many people have a need to share their experiences with others, and may gain comfort from talking them over with a supposed other being. There is much in common between personal recollection or anticipation, discussion with another person, and some forms of prayer. Of course many believe that the god to whom they pray can and will answer their prayers. Indeed, in addressing a deity it is almost impossible not to believe that a response will be forthcoming, just as when one speaks to a friend one is sure he will reply: faith in a god's responsiveness is built into the very act of praying. And if the supplicant has any doubt, he may invent reasons why a response should not be forthcoming—sins not repented, or the very fact of doubting, for instance. Prayer can also be seen as worship, but worship seen as a *quid pro quo* for benefits received or expected, as part of the reciprocal relationship with the deity. Such a relationship can have close parallels with inferior/superior relationships in everyday life.

Sacrifice, like prayer, implies a relationship between the sacrificer and the deity. The act of sacrifice can be seen as a symbol of relative status, comparable to paying homage, or as a symbol of devotion or love. In other cases the focus is on the hope of long-term gain or the avoidance of disaster: just as a human relationship may involve incurring current costs in the hope of long-term gains, so sacrifice to a deity can be seen as a symbol of trust in the deity that rewards will be coming (or disasters forestalled) in the long run.

Sacrifice may also involve social elements—both to display the participant's own religious devotion and to demonstrate to others how much he can afford to give to the gods. In the latter case, sacrifice may be analagous to what is known to biologists as the Zahavi effect: extravagant ornaments like the peacock's tail have been selected in evolution because they indicate that the bearer can afford to sustain them (Zahavi, 1977).

Analagously, some humans display their status by demonstrating what they can afford.

4.4. The Forms of Ritual

The forms of religious ritual exploit many human characteristics and propensities seen in everyday life. In the first place, there are many parallels with the repetitious rhyming songs and games played by children, not to mention the superstitions that children's games often involve. The pathological obsessive/compulsive rituals of adults also have much in common with some religious rituals, such as repetitive chanting or the manipulation of a rosary (Marks, 1987).

The finer details of religious ritual performances play on a number of human behavioural propensities. The gestures used, the exaggerated forms of movement and vocalisation, play on human perceptual mechanisms to make the ceremonial more impressive: similar mechanisms are involved in secular, and especially military, ceremonials. Some of the symbols and artefacts used are also related to basic human propensities. By virtue of their material, workmanship, and associations they engage the attention of those present. Light and radiance and valuable materials draw the gaze, and may symbolise purity and power. In many Christian churches the chalice used in the celebration of Mass is made of valuable materials, often decorated with precious stones, and is of a shape associated with tradition. The gesture of elevating the chalice marks the moment of consecration.

The sequence and form of most religious rituals are related to the occasion and to the beliefs and narratives of the religious system. For example, *rites de passage* can be divided into preparatory, transitional and concluding phases, so that they are in effect themselves narratives. Traces of these are still to be found in the Church of England ceremonies of baptism and confirmation while, in a longer time frame, the years between baptism and confirmation can be seen as a transitional period during which responsibility for the child's spiritual well-being is taken over by the godparents. The same three phases can be distinguished in the marriage service. Of course the fact that three phases can be distinguished in most *rites de passage* is hardly surprising: the point being made is that the form of the ritual is related to its role in society.

One important difference between everyday action sequences and many religious rituals lies in the nature of the links between the subsequences. Most everyday activities can be analysed into a succession of sub-activities directed towards sub-goals necessary for the overall goal (Miller, Galanter, & Pribram, 1960). In many ritual sequences the

sub-sequences are not describable in terms of sub-goals, but simply have a fixed position, deviation from which invalidates the ritual (Boyer, 1994).

5. CODES OF CONDUCT

It would be possible to formulate an almost infinite number of codes of conduct, ranging from the most altruistic to those based on the self-assertive principle of "Damn you George, I'm alright". Religious systems usually include a moral code—precepts about how one should and should not behave—which most participants internalize and incorporate into the self-system. The term "moral code" involves a value judgement—it implies that the code has the approval of at least most members of the group in question, individuals labelling events along a good/bad continuum. The criteria they use come to feel natural, and the codes of conduct of other cultures may become unacceptable and even incomprehensible. The development of any code of conduct is complex, but in a mature form must require a "theory of mind" (that is, an ability to interpret the behaviour of others in terms of intentions), and the ability to empathize. Both of these, though involving complex developmental processes, can be seen as basic human characteristics, potentially present in all but developed to a different extent in different individuals.

In the present context interest must focus on the content of the moral code. It is often said that science cannot provide a value system but, if one accepts that it is not imposed or validated by a deity, every value system must come from somewhere. Codes are rarely, if ever, suddenly acquired, carved in stone. Rather they develop over time, with mutual influences between what people do and what it is thought appropriate for people to do. Any system of values must have been selected over time from a range of conceivably possible ones, and science has a part to play in understanding the processes involved.

Most moral codes include at least three overlapping categories. The first involves rules about behaviour towards supernatural entities: included here are the first four Hebraic Commandments, and admonitions concerning the status of the priests or other religious specialists. It is in the interests of the latter to see that they are upheld, and they can thus reasonably be ascribed to the status-seeking propensities of a category of individuals.

The second category, which overlaps with the others, concerns the maintenance of the religious and social group. These may overlap with the first group ("Thou shalt have none other gods but me") or with the third ("Thou shalt not kill", usually taken to refer to in-group members).

Directives about ritual performance and dietary prohibitions may also be included here, or may be seen as a separate category.

The third category concerns the behaviour of individuals to each other, and is the one of most immediate interest in the present context.

Moral codes can be seen as constraining individual behaviour in a way that makes social life possible—though they may be such as to advantage some individuals over others. Although prescriptions about social behaviour differ widely between cultures, many of them can be seen as reducible to a few basic issues. The most important of these seem to be the principle of "Whatsoever ye would that men should do unto you, do ye even so to them" (Matthew, 7:12), or "Love thy neighbour as thyself"; principles concerned with self-assertion and the establishment and maintenance of hierarchical relations in society; principles concerned with the regulation of sexual behaviour; and principles concerned with the maintenance of in-group/out-group differentiation. Of course such principles must become part of the socio-cultural structure, and must be compatible with other aspects of that structure. They may be influenced by historical and ecological factors.

Consider first the matter of reciprocity. The moral codes of all the world religions contain precepts requiring individuals to behave to others as they would like others to behave to them (Küng & Kuschel, 1993). There is a good deal of evidence that the principle of Do-as-you-would-be-done-by is an apt description of some aspects of within-group interactions of some non-human species, and there is growing evidence that this is the result of natural selection (e.g., Wilkinson, 1988). Many social animals also incur costs (assessed in biological terms, i.e. effects on survival and reproduction) if doing so benefits individuals genetically closely related to them, an obvious example being the readiness of parents to sacrifice their own interests for the sake of their offspring. Many animals are also willing to incur limited costs if doing so benefits those likely to reciprocate by helping them in the future. Although it seems at first sight unlikely that unselfish behaviour would be maintained in a population, because selfish individuals would be likely to do better than unselfish ones, it has been convincingly argued that selection within and between groups could favour in-group cooperation provided that the group is not too large and that offspring tend to acquire the behaviour traits that are most prevalent in the population. The latter is especially likely to occur if the consequences of the behavioural trait are difficult to discern (Boyd & Richerson, 1991).

Similar principles apply to humans. Empirical evidence shows that individuals are more willing to incur costs to help those whom they perceive to be related to them and those likely to reciprocate in the future. Indeed these two principles are likely to be linked, since A's readiness to

incur costs for the sake of B will depend on A's perception of the genetic relatedness between A and B and on his/her assessment that B will reciprocate, and the latter will depend on B's perception of their relatedness. The most prominent theories of human relationships, namely exchange theories such as equity theory, are based upon the premise that interpersonal behaviour is based on a norm of reciprocity (Walster, Walster, & Berscheid, 1978). A number of studies of relationships have shown that partners may feel uncomfortable if they perceive themselves to be either under-benefitted or, interestingly, over-benefitted (Prins, Buunk, & VanYperen, 1993). Of course in real-life relationships reciprocity is rarely immediate: the establishment of a close relationship involves incurring costs in the hope of future gains. Trust in the partner, and seeing the partner as committed to the deal or to the relationship, are thus essential (Hinde, 1997). In the case of a relationship with a god, trust is equivalent to faith.

It is primarily the principle of reciprocity that provides a common basis for all moral codes and is responsible for making group living possible. There is every reason to suppose that variants of this principle apply in all cultures, and the biological parallels suggest that a propensity to show reciprocity is a product of natural selection. Other pan-cultural psychological characteristics facilitate the maintenance of reciprocity. Thus experiments show that individuals are adept at detecting infringements of social contracts (Cosmides & Tooby, 1992). Furthermore, humans are equipped with emotions important in regulating exchange, such as anger, shame, and guilt. The two latter are minimally present in other species, and must surely have been selected in evolution to facilitate equity in social relations. We feel anger if we perceive ourselves to be under-benefitted and moral outrage if we see others infringing social contracts. How far these depend on experience in development is an open issue, but they would seem to be universal human characteristics.

The second important influence on moral codes is a consequence of the efforts of individuals to assert their status. Most moral codes involve precepts concerned with behaviour appropriate to the individual's position in society. Respect for parents and ancestors can be seen as one form of this, but the code may reach much more widely. The Anglican Catechism requires the confirmand to recite his duties. Amongst the duties to the neighbour are "To honour and obey the King, and all that are put in authority under him: To submit myself to all my governours, teachers, spiritual pastors and masters: To order myself lowly and reverently to all my betters . . . and to do my duty in that state of life, unto which it shall please God to call me." Such precepts were probably originally imposed by high status individuals or groups, and can lead to conflict: their maintenance may depend on the originators using power, guile or persuasion to convince others that the rules are in their own best interests—or, perhaps more

usually, invoking supernatural authority. Such precepts may also be affirmed by those lower down preferring that their current status should be maintained rather than that the *status quo* should be upset.

The third source of moral codes concerns the regulation of sexual relations. While every culture has its own rules for regulating who may engage in sexual behaviour, these usually seem to be such as will augment reproduction. Thus a prohibition of intercourse during menstruation may serve to increase its frequency during the fertile period. Many of the rules can be related to the efforts of men to prevent themselves from being cuckolded. The evidence for this has frequently been reviewed elsewhere (e.g., Alexander, 1979; Buss, 1994). Empirical studies indicate that male jealousy tends to centre round sexual issues, female round the transfer of resources (Buunk, 1995). Other rules concern the eligibility of marriage partners, and many of these are such as to avoid the disadvantages both of too close inbreeding and of too distant outbreeding: however not all such rules can be interpreted in this way.

A fourth issue concerns the maintenance of ingroup/outgroup distinctiveness. All humans tend to behave differently to individuals whom they see as belonging to their own group from the way that they behave to outsiders (Tajfel, 1978), often extending to members of their own group attitudes more appropriately shown only towards relatives, so that the entire in-group is treated as though related. Thus the welfare of in-group members may become almost as important as if they were close blood-relatives, and ingroup/outgroup differentiation may be in part a consequence of kin-selection (Johnson, 1986; Hinde, 1989). Most moral codes require standards of behaviour towards in-group members that differ from the standards of behaviour directed towards outsiders. In the Hebraic code it is the neighbour's house and wife that must not be coveted, and then as well as in our own society killing of out-group members is encouraged in wartime. This issue is clearly illustrated by the savagery with which the Israelites are said in Deuteronomy to have behaved towards their enemies. Jesus himself showed an ethnic bias, and it was only after his death that the Apostles addressed themselves to Gentiles.[2]

[2] Indeed the willingness to show benevolence to out-group members has had a chequered history in our own society. Too often, in the past, people perceived as different have been seen as threatening, and people perceived as threatening have been seen as different. The difference between our own moral code and the codes of conduct of others often lies in where the limits of neighbourhood are placed. Now we know that the criteria of colour and race by which outgroups have been distinguished are superficial and misleading in that they do not represent fundamental differences, and science is helping us to see that religious differences are also not differences in basic humanity. There is thus hope that the propriety of extending the principle of reciprocity to all humans (and even to animals) can be accepted more and more widely. But some preferential treatment of those seen as related is likely to remain.

Thus some aspects of moral codes are such as to maintain group distinctiveness. The dietary prohibitions of Leviticus have been given diverse interpretations, but it seems unlikely that effects on health were primary and more probable that their main purpose was the maintenance of group distinctiveness. Similarly the practice of circumcision, carried out on the eighth day, has been regarded as of great religious significance, representing part of Abraham's covenant with God, and is a sign of group membership. As might be expected, such precepts are more characteristic of cultures in which the religious system is seen as "belonging" to the group than in the proselytizing religions like Christianity.

Of course cultures differ in the way in which these principles are interpreted and in how they accomodate to the status-seeking of individuals. For instance, as a broad generalisation the emphasis on status-appropriate behaviour is more marked in eastern religions than it is in the west. Religions differ also in the addition of precepts relating to local conditions and to the maintenance of the social system.

Now if a moral code is seen as bequeathed by a supernatural authority it must be accepted, and a major part of the religious specialist's role is to affirm that impression. But a moral code is continuously evaluated by the members of the society, and individuals may differ in their conclusions. In her (or his) attitude to the code, each individual will be influenced by her own predispositions and experience, mediated by her ability to interpret the behaviour of others and to empathize. The propensity for behaviour to be guided by the principle of reciprocity will push the code towards behaviour conducive to the common good, but this will always be in conflict with the self-assertiveness of individuals. The vigour of such debates fluctuates with time, but whether they concern the propriety of throwing Christians to the lions or the rights of the unborn child, differences of opinion are likely to be present. However the bases for evaluation will be criteria of the same nature as those by which the code evolved in the first place—reciprocity, status-seeking, regulation of sexual behaviour, group distinctiveness, and possibly others, influenced by tradition and by local conditions—with the details of their application changing with the social and environmental conditions. Just because social and environmental conditions change, and just because individuals' emphases on their own good inevitably often conflict with the common good, codes change with time and differ between societies. Religious specialists can provide a stabilizing influence, but only if their teachings are accepted.

There has been a long debate as to whether there are universal standards of morality, or whether ethical questions should be judged against cultural norms. The approach adopted here requires neither of these two extremes. Rather it is suggested that all codes are based on pan-cultural propensities, with cultures differing in the way in which the principles are

interpreted and in the addition of precepts relating to local conditions and to the maintenance of the particular social system. This means that the code of conduct that emerges is not necessarily the best for all people—it may be engineered by one sub-group to exploit another. And when we see such exploitation, we see it as incompatible with our own moral code, and rightly condemn it. Values are thus neither completely relative, nor universal and intrinsic to human nature. But a scientific approach can in principle at least bring understanding of how moral codes evolve, and that brings morals within the scope of science.

There is, of course, a further problem. The fact that a moral code can be understood as viable in scientific and social scientific terms does not necessarily mean that people will accept it. One of the most important concomitants of religion has been its implication that the moral code is divinely given. Those who infringe it may seem to be temporarily better off, but they will get what is coming to them at the Judgement Day. But if people drop out of the religious system, how is the moral code to be upheld? Will not those who try to foster it be seen as autocratic "Big Brothers"? This is still a major problem—perhaps the most fundamental that humankind has to face. I suggest that it is not beyond science: we are increasingly able to forsee the probable consequences of alternative precepts and such predictions can be fed into the continuing dialectic between the current code and the collective mind.

6. RELIGIOUS EXPERIENCE

Religious experiences are perhaps the most difficult aspect of religious systems to fit into a biological background. William James (1892) described them as "the feelings, acts, and experiences of individual men in their solitude, so far as they apprehend themselves to stand in relation to whatever they may consider the divine". But religious experiences are so diverse that no definition adequately comprehends them, and William James's definition undoubtedly reflects his own cultural background.

That such experiences are quite widespread cannot be doubted. Research initiated by the late Sir Alistair Hardy, formerly Professor of Zoology at Oxford, has clearly demonstrated this, in that requests for reports elicited thousands of replies. Several kinds of religious experience have been recognised: mystical and ecstatic experiences, paranormal experiences, charismatic experiences, regenerative experiences, and so on, and it is difficult to draw a line between religious experiences and those of a more secular nature.

Heuristically useful here is a distinction between the technique by, or the circumstances in which, the experience was induced, the nature of the

experience itself, and its interpretation. The distinction between religious and certain secular experiences seems to rest on the interpretation made by the individual concerned. Certainly, within experiences categorised as religious, the reported imagery is closely related to the subjects pre-existing religious beliefs, though on occasion (as with St. Paul on the way to Damascus) those beliefs may have previously been suppressed. There are clear resemblances between religious and aesthetic experience, and also links to responses to landscapes likely to have been congenial to our evolving ancestors (e.g., Orians & Heerwagen, 1992). But similarities between supposedly religious and secular experiences could be evaluated only if one could assess the experiences shorn of their interpretations—probably an impossible task.

7. SOCIAL ASPECTS

The social aspects of religious systems have been mentioned several times and need no further discussion here. Religious beliefs depend in large measure on consensual validation from others, and religion totally without social influences is almost impossible to imagine. The feeling of communal belonging brought by religious observance is important to many, and common beliefs and practices can unite communities.

8. RELIGION AND DARWINISM

The aim of this essay has been to see how far religious systems could be seen to depend on pan-cultural human propensities. Perhaps it would be as well to repeat that there is no suggestion that the tendency to subscribe to a religious system is itself an adaptive characteristic, nor that every one of the propensities that have been mentioned are or have been adaptive. The suggestion is simply that the potency of religious systems depends, at least in large measure, on pan-cultural human propensities. The principal ones that have been mentioned may be summarised briefly.

Religious beliefs can satisfy certain ubiquitous human needs. The need to be able to *attribute causes to otherwise incomprehensible events* can be satisfied by an impersonal god, and that for *perceived self-efficacy* by an intervening god. Needs usually met in personal relationships, such as *felt security*, and the related *desire for survival* after death, require a personal god. The belief system may also satisfy various other needs usually met in *interpersonal relationships*. Attraction to others with similar beliefs provides

also *consensual validation* of the beliefs and a *sense of community*. Beliefs are usually acquired in the course of *socialisation*, and their form involves the tendency to postulate *animate/anthropomorphic causes* for events, with the assumption that *animate beings have essential natures*. There is a general human tendency to use a *narrative* form.

Rituals depend on or affect the *self-system* and *social identity*; *responsiveness to salient stimuli, seeking arousal; material objects as symbols, often of status; status-seeking; dramatic participation, the sharing of experience, etc.*

The ethical system involves abilities for *"theory of mind" and empathy, preference for kin, reciprocity, equity, and associated behaviour and emotions including trust, anger, cheater detection, jealousy, guilt, and shame; status-seeking, aspects of sexual behaviour*; and the *maintenance of ingroup/outgroup differentiation.*

Religious experience is probably related to aesthetic experience, which may be related to *habitat selection.*

There is no suggestion that these are entirely independent characteristics, nor that their development is independent of experience: it is claimed only that it is reasonable to suppose that they are universal human characteristics—as yet we know little about their ontogeny or inter-relations. Indeed real understanding of the biological bases of human behaviour requires, perhaps above all else, a greater understanding of its ontogeny. Nor is it suggested that this is a complete list. However what this does show is that the manner in which religious systems satisfy or express universal propensities goes a long way towards explaining their prevalence.

To that must be added that the inter-relations between the components also support the persistence of the system. The narratives support the structural beliefs and convey the values. Ritual is also related to the structural beliefs and narratives and purveys the values, and may provide a background for religious experience. The values are closely tied to the social aspects of the system.

9. CONCLUSION

Given that religion satisfies so many human propensities, it is surely legitimate to ask how much the erroneous beliefs matter. Whether we recommend that the whole system be discarded should surely depend on whether we can replace it with something better. A scientific approach is incompatible with the belief system, but societies need some means to sustain their moral codes. Many feel that current social problems stem in part from decreasing standards, and these in turn from the decreasing

effectiveness of religion in everyday life. Of course there are also other factors—for instance the increase in the scale of society such that values that could be effective in small communities are no longer so. The disruptive forces in society are becoming almost more than community impulses can cope with. Merely espousing moral standards is unlikely to be effective, because moral codes cannot merely float in society—they need an anchor in the shape of a way of thinking, an orientation to life. We must as a matter of the utmost urgency seek for a new one that does not fly in the face of empirical evidence and can take the place that religion has held. But in the meantime, the pragmatic course may not be to take a purely destructive attitude to other people's views, but try to understand why they hold them. This may sound like prescribing a temporary panacea for the less well informed, but it is clear that a new orientation will not come in a generation or two, and in the meanwhile societies must be held together. Societies have always changed and will continue to change, so this is not just an issue of hanging on to the past—but we should now be in a position to see that some changes are desirable and others are not.

10. NOTES

An earlier version of this paper was presented to the British Humanist Association under the title of "Religion and Darwinism" (1997). A longer version has been published ("Why gods persist: a scientific approach to religion" (1999). London: Routledge).

I am grateful to many colleagues, especially Helena Cronin and Jessica Rawson, who made many comments on an earlier draft, and several members of St. John's College, Cambridge, with whom I have discussed aspects of this paper.

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